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Understanding and Predicting Tree Growth

Edited by

SUNE LINDER

Section of Forest Ecophysiology
Swedish University of Agricultural Sciences
S-750 07 Uppsala, Sweden

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES
COLLEGE OF FORESTRY
UPPSALA SWEDEN

The present volume contains the papers presented at a SWECON workshop "Understanding and Predicting Tree Growth" in September 1979. The papers cover different aspects of tree growth modelling from the stand level down to the level of cambial activity.

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Preface

During the last two decades there has been intensive research concerning the physiology of trees. The main incentive for a diversity of activities has been the premise that increased knowledge of the production processes is the best and only way to an increased and sustained forest production. During the same period the use of systems analysis and modelling within biology have become accepted and common tools. However, the construction of adequate growth models, based on often detailed information of physiological processes, has proved to be much more time-consuming and difficult than expected. The modelling efforts have also stressed the need for more and better information on the physiology of trees under 'natural' field conditions.

This report contains the papers presented at the SWECON workshop, "Understanding and Predicting Tree Growth" at Jädraås in September, 1979. As a result of the discussions and ideas presented at the workshop all papers have been rewritten, which is one of the reasons for the delay with the publishing of the proceedings. The workshop included daily poster sessions and the 34 posters presented were published in an earlier report (Linder, S. (ed.) 1980. Swed. Conif. For. Proj. Tech. Rep. 25, 155 pp.)

The workshop was initiated by Prof. P. G. Jarvis, Dr. E. D. Ford and myself as part of the cooperation that has existed between our research groups for more than ten years and was sponsored by the Swedish Coniferous Forest Project (SWECON). I was assisted in the planning of the workshop by Dr. G. I. Ågren and Dr. B. Axelsson to whom I want to express my sincere gratitude. Mr. B. Andersson and Mr. E. Lindquist took care of all the practical details during the workshop and their support was of vital importance for the success of the meeting. Thanks are also due to all my colleagues who have acted as referees for the papers included.

Sune Linder

Contents

Problems Involved in Modelling Tree Growth

G. I. Ågren

Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden

Abstract

The problems and possibilities of constructing growth models are discussed using five published growth models as a starting point. The models are compared with respect to their structure and formulation of processes. It is only occasionally that the five models agree in their formulations. These different opinions are evaluated against experimental studies and it is found that generally the experimental studies do not permit a definite decision as to which of the different formulations that is to be preferred. It is concluded that the time is not yet ripe for the use of larger simulation models to handle growth problems. The present research should instead be directed towards analysing more specific phenomena.

Introduction

During the last few years the use of simulation models to mimic the behaviour of ecological systems has become very popular. As a result there now exist a number of books with titles like Simulation in Ecology, and there is also a new journal entirely devoted to this subject, Ecological Modelling. Some of these studies have, of course, dealt with trees or forests and from these I have selected some for use as a basis in discussing a number of problems involved in modelling tree or forest growth.

Depending upon the objectives, models look very different. As a first broad categorization one can talk about managerial models and explanatory models. The models intended as management tools generally rely upon regressions to describe tree growth and the problems the modeller has to face are essentially statistical and concerned with the adequacy of the data base. Explanatory models can be subdivided into two categories, general och specific models. Specific models focus upon only a single aspect of growth, treating other factors perfunctorily. Examples of such models are a model by Fagerström and Lohm (1977), describing the effect upon tree growth of the nutrient dynamics in the needle biomass of Scots pine, and the matrix model of forest succession by Horn (1975). In my opinion, such models are useful in that they provide a valuable contribution to the understanding of the specific process upon which they concentrate. I would like to see more models of that kind in the future. I will not, however, discuss them any further here; subsequent discussion will be confined to the general models. By general models I mean models that are claimed to include several, if not all, of the essential processes connected with tree growth and in a way that is said to represent biological mechanisms. Typically, these models are formulated as simulation models with measured time series of climatic data as driving variables.

To illustrate the problems involved in modelling tree growth I have selected five models rather arbitrarily from the literature. My purpose is not to review tree growth models but to show how different people perceive the difficulties in formulating appropriate process descriptions. As will be seen, the importance attached to different processes varies widely between modellers. Consequently, the amount of supporting information for a particular process description also varies greatly. The five models selected are:

1. TEEM: Terrestrial Ecosystem Energy Model (Shugart *et al.*, 1974). A model describing the development of a single-species forest over a few years. Structurally this is the simplest of the models. The

model consists of three submodels; a primary production submodel, a decomposition submodel and a consumer submodel. It is only the primary production submodel that will be discussed here.

2. SIMED: SIMulation of *MEDicago* growth (Holt *et al.*, 1975). Although this model applies to an agricultural crop (alfalfa) I have included it to show the principal similarities between agricultural crop models and tree growth models.
3. SDF: Simulating a Deciduous Forest (Sollins *et al.*, 1976). This is a model for a forest of three "species": yellow poplar, other overstory trees, and understory. It also contains a submodel for decomposi-

Table 1. Comparison of five growth models. +(−) indicates the presence (absence) of the variable in the model. +/− indicates that in certain versions this variable is present. The number of parameters and time steps are for some models given only approximately. To simplify the comparison some variables are not those used in the original model but have been replaced by similar ones.

PROPERTY Extension Species	CERES Stand Oak	PT Tree Scots pine	SDF Stand Yellow poplar + others	SIMED Stand Alfalfa	TEEM Stand Deciduous trees
Number of state variables	10	11	13	6	4
Substances	C	C, N, H_2O	C	C	C
Number of parameters	>53	78	>63	90	>35
Equations	Difference/ Differential	Difference	Differential	Differential	Differential
Time span	A few days/ a few years	1 year	1 year	1 month	2–3 years
Time step	1 h	1 d	1 h	1 h	Not reported
Structural variables					
Leaves	+	+	+	+	+
Branches	−	+	−	−	−
Stem	+	+	+	+	+
Roots	+	−	−	+	+
Large roots	−	+	−	−	−
Fine roots	−	+	+	−	−
Buds	−	−	+	−	−
Fruits	+	−	−	−	−
Number of carbohydrate storages	6	1	1	3	1
Water	+/−	+	−	−	−
Nutrients	+/−	+	−	−	−
Climatic variables					
Radiation	+	+	−	−	+
Air temperature	+	+	+	+	+
Soil temperature	−	+	−	−	−
Soil water potential	−	+	+	−	−
Relative humidity	+	+	−	+	−
Soil nutrients	−	+	−	−	−
Photoperiod	−	+	−	+	−
Processes					
Gross/Net photosynthesis	N	N	G	G	G
Growth/Maintenance respiration	M	G&M	M	Lumped	G&M
Translocations	+	−	−	+	−
Mortality	+	+	+	−	−

tion, which will not be considered in this article.

4. PT: Production Tree (Axelsson & Ågren, 1976) (see also Ågren & Axelsson, 1980). A model for the growth of a single tree (Scots pine) during one year. The most complicated of the five models and with the highest ambition of being all-including.
5. CERES: (after a Greek goddess) (Dixon *et al.*, 1978). A high resolution model to predict effects of perturbation.

Some principal properties of the five models are summarized in Table 1.

Model structure

The first aspect that requires consideration when modelling is the structure of the model. Typical of the models discussed here is their dynamic character with several feed-back loops. Another common feature is the non-linear form of the equations describing interactions. None of the modellers even consider the possibility of linearizing the equations. The reason for this is obviously that all the authors are interested in models where the state variables show large variations rather than small disturbances around some equilibrium value. Four of the five models are formulated as differential equations instead of as difference equations (PT). However, in practice this is an aspect of no consequence as all the models are analyzed by simulating their behaviour on computers in a way that makes the differences between differential and difference equations disappear.

The differences between the models appear when we consider the state variables that are defined. Which are the storages that need to be handled separately? Comparing the five models we recognize that this simple question caused appreciable disconcert. The only point upon which the five models agree is that a tree requires foliage (in PT the foliage has even been represented by four state variables). There is general agreement between the authors of the models that one should distinguish structural material from metabolizable substances (often termed carbohydrates), although this is only commented upon in the discussion of SDF but not implemented in the model. In one of the models (CERES) the metabolizable substances are even divided into two classes, sugar substrate and storage, of which only the first can be translocated within the tree. The question of translocations is also handled differently in the models. In two of them (CERES and SIMED) there are three compartments for carbohydrates associated with foliage, stem, and roots respectively, whereas PT and TEEM lump all the carbohydrates into one single pool for the entire tree. Partly, this can be understood as a consequence of the different time steps used in the models, one hour and one day, respectively. However, in no case there is any thorough analysis of the need to reckon with translocations. Only in PT a reference is made to a study (Watson, 1975) indicating fairly high translocation rates, which is used as an argument for not using several carbohydrate state variables. Since important seasonal variations in the composition and amounts of the carbohydrates are known (e.g. Ericsson, 1979) it is of course interesting to know whether transformations between active forms and forms just for storage can be limiting for growth. It is worth noticing that in CERES, formation of wood is assumed to take place not from the mobile sugars but from storages.

The five models differ with respect to the substances required to describe tree growth. Two of them (SDF and SIMED) consider only flows of carbon – in SIMED it is explicitly stated that water and nutrient availability is assumed optimal whereas in SDF these questions are passed without comment. In TEEM, plant water potential is included as a regulating variable but it is nowhere stated how its influence operates. Nutrients are not discussed at all although the model contains a submodel for decomposition. CERES is developed in several versions, in some of which nutrients and water are included, but the version to be discussed here is one that deals only with carbon flows. In PT, finally, nutrients (represented as nitrogen) and water are included as separate state variables. With agricultural crops, as alfalfa, subjected to intensive fertilization and irrigation, it is

perhaps reasonable to assume water and nutrients to be available in, if not optimal, constant supply and their exclusion from SIMED is thus reasonable. In forests the storage of nutrients in the vegetation is possibly sufficient to buffer against short-term (a year) variations in nutrient availability, thereby alleviating the necessity of including them in these models. The water supply in a forest may, on the other hand, definitely show such variations that it seems imperative to include some water variable explicitly in tree or forest growth models (Jarvis, 1981).

Statement I: Our present state of knowledge does not warrant the high resolution often used in today's tree growth models. A fruitful approach might be to leave the within-day (or even within-year) resolution and look for the development over several years. In such models one can concentrate upon the most dynamic state variables – leaving perhaps just one, the leaves. All process descriptions would also be greatly simplified, making it possible to test different phenomenological formulations. Depending upon the climatic conditions, water and nutrients could also be eliminated from the model.

Processes

The most important parts of the simulation models are of course the process descriptions. In the five models discussed in this article both similarities and dissimilarities exist. I will here go through the most important ones and look at the different approaches and try to give an idea of how well founded I think the different formulations are. It is obvious that the levels of knowledge about the different processes vary enormously, something that must be recognized when considering growth models. One of the most striking facts is the sometimes fairly good knowledge at a biochemical or detailed physiological level but where the bridge to an entire organism is completely lacking.

Water uptake and transpiration

At the levels of ambition of the presently discussed models the two processes – water uptake and transpiration – can be considered as fairly well understood. Several simulation models describing them have also been developed (e.g. Goldstein *et al.*, 1973). The main difficulty one can encounter when implementing them in growth models is their tendency to dominate the model and their requirement of short time-steps (typical of the order of one hour) to behave stably. As a consequence, the programs will be slowed down, possibly to an extent that is unacceptable in order to allow the main focus of the simulation to be placed upon the growth processes. Other difficulties are the demands for high resolution of the driving variables, which of course can be circumvented by different interpolation techniques. Also the information about root distribution may be much less than the amount desirable to fit the requirements of the model. However, in principle, the difficulties with these processes lie mainly on the technical plane – not the conceptual one. Of the five models discussed in this article, only one includes these two processes (PT); in other models (CERES, SDF, SIMED) water status is represented by exogeneous variables.

Statement II: Models concerned with water transport can be constructed with a high degree of sophistication. This opens the possibility of investigating effects of the water variable, maybe not on growth directly, but rather as its potential as a growth regulating factor. Some problems that I think should merit further investigation are the effects of increasing tree size, in height as well as in leaf biomass, on the turnover of water in the forest.

Nutrient uptake and loss

These processes have long been a major obstacle when trying to build comprehensive growth models. The modelling of nutrient uptake has been restricted by ignorance about nutrient availability in the soil. Once the nutrients were available in the soil, more or less sophisticated models for calculating their uptake have existed for some time (e.g. Baldwin

et al., 1973). Recent work by Bosatta *et al.* (1980) has, at least for Scots pine forests, given important information about the time course of soil nutrient availability which could be incorporated in a growth model. The processes associated with nutrient losses have attracted much less attention, but for modelling purposes one can probably in most cases be content with a simple formulation based upon a (fixed) concentration in material that is lost from the the plant. It is also possible that the nutrient dynamics is relatively slow, such that the annual course of nutrient uptake and loss need not be defined very precisely as long as the total amounts taken up and lost over the year are correct. However, this proposition remains to be tested – for example in a special model. Since nutrients (nitrogen) are treated as a state variable only in PT, it is also only there that these processes are included.

Statement III: Nutrients are tricky, but I see some progress under way (cf. Ingestad *et al.*, 1981). The weakest link here will long remain the description of the nutrient flux density in the soil and the influence of the vegetation upon it.

Photosynthesis

In the domain of growth modelling the photosynthesis processes are probably those that are the best understood and for which the best submodels exist. Certainly, these submodels often contain important parts that are only phenomenological and not truly mechanistic in their formulation, but as long as they are to serve as submodels in a more complex environment this is acceptable. An example of a model of this kind is the FAST-model by Lohammar *et al.* (1979, 1980).

Although the basic principles of photosynthesis are known the five models discussed in this paper differ substantially in their descriptions of the photosynthesis. A first distinction is between models operating with net photosynthesis (CERES and PT) and those having gross photosynthesis and photorespiration (SDF, SIMED and TEEM). In practice this explicit sorting out of the photorespiration has no consequences because no use is ever made of the specific properties of photorespiration. A second distinction found between the models is in their treatment of light interception. Some of the models (SIMED and PT) do not account for light interception explicitly but argue that with the crude formulation of the photosynthesis used one might just as well let such a factor be included in the general description of the photosynthesis. The other models (CERES, SDF and TEEM) have different ways of including the effect of a varying leaf area index upon photosynthetic rates. In CERES an average light intensity within the canopy is estimated while the other two models assume a horisontally uniform canopy and then an integration is performed over the canopy, much to the pleasure of the modeller who for once can do some analytical calculations. Such an approach is perhaps reasonable in dense canopies. However, in sparse conifer canopies, such as the one modelled in the PT-model, where the horisontal heterogeneity is considerable and at the same time there are several year-classes of needle with different photsynthetic efficiencies, the validity of the approach is much more questionable.

Statement IV: Photosynthesis is definitely so well understood (cf. Linder & Lohammar, 1981) that the time is ripe for utilization of models of photosynthesis to ponder about effects of climatic variations between years upon net photosynthesis and from there possible effects upon growth.

Respiration

From the biochemical point of view respiration is one of the best understood processes involved in growth modelling. A common approach is to consider the respiration as consisting of two distinct parts, one associated with the maintenance of the living tissue and one associated with its growth. Penning de Vries (1974, 1975) has made extensive theoretical calculations on these processes, giving minimum estimates of their energy requirements. The idea of differentiating the respiration into two components has been

contested as lacking biochemical significance (Lambers, 1979). Yet with a phenomenological approach the idea of two different respiratory processes is attractive, giving a possibility of estimating the energy costs in a well-defined manner. However, of the five models discussed in this article only two of them (PT and TEEM) deal with these two respiratory processes separately. CERES and SDF consider only a maintenance respiration, ignoring that building up a complex molecule from simpler ones requires energy. In SIMED again only maintenance respiration is discussed and it is concluded that the extra information required to meaningfully treat the two processes separately is not available and a simpler description therefore suffices.

The difficulties involved in applying the principles discussed by Penning de Vries (1975) as to the magnitude of the respiratory components can be illustrated with an example. The most important contribution to the maintenance respiration comes from the need to maintain the proteins in the cells. According to Penning de Vries's estimates, 0.07–0.13 g C (in the form of glucose) $(g\ N)^{-1}d^{-1}$ is required for protein maintenance at about 20°C. Now, a young Scots pine (*Pinus sylvestris* L.) can contain around 25 g N, thus requiring 1.75–3.25 g C for its daily protein maintenance during summer conditions. Assuming such a rate of maintenance respiration for 100 days then means an annual maintenance respiration of 175–325 g C, which should be compared with an estimated net photosynthetic production of 3100 g C y^{-1} for the same tree and a measured total respiration of 140–220 g C. Hence, neglecting all other respiratory processes the theoretical estimate barely fits within the experimental range. However, for a nearby tree, subjected to intensive fertilization/irrigation, the situation is more complex. This tree contains 40 g N, giving a theoretically estimated respiration of 280–520 g C, which should now be compared with the estimated photosynthesis of 2500 g C and the measured respiration of 190–230 g C. The theoretical estimates are based upon an assumption of maximum biochemical efficiency and thus minimum estimates, but in this case the values of the respiration are clearly too high. Lambers (1979) found these theoretical estimates on the contrary to be by far too low for a series of other species.

Statement V: Respiration has been dealt with extensively from a biochemical point of view but as shown above, it is hard to match this knowledge with field observations. To make this connection from small-scale laboratory conditions to complex field situation should be a real challenge. On the other hand, respiration seems to be only a minor component in the carbon budget of forest trees (cf. Ågren *et al.*, 1980), and is therefore perhaps uninteresting when working with growth models.

Growth control

The crucial process in growth modelling is of course the growth process in itself. Unfortunately, this is the process about which the least is known and understood, the first obstacle often being the lack of precision in the definition of what is meant by growth. In this article I use the word growth to mean irreversible incorporation of carbon into structural material. A lot of factors are known (or imagined) to regulate this process but not very much detail is to be found in the scientific literature. Table 2 summarises which factors the modellers have thought necessary to correctly describe the growth process. As can be seen there is only one factor that everyone agrees upon as necessary, carbohydrates; all the other factors seem more or less dispensable. I will now discuss these factors more in detail.

Carbohydrates

Since carbohydrates form the major constituents of biomolecules it is quite natural that they should have an influence upon growth. Obviously, when there are no carbohydrates there can be no growth, and so far everyone agrees. Then the opinions diverge. In two of the models (SDF and CERES) the growth rate is assumed proportional to the carbohy-

Table 2. Comparison of five growth models. +(−) indicates that the factor has (has not) a direct influence upon the growth process.

FACTOR	CERES	PT	SDF	SIMED	TEEM
Carbohydrates	+	+	+	+	+
Water	+	+	−	+	−
Nutrients	−	+	−	−	−
Temperature	−	+	+	+	−
Time (phenology)	−	+	−	+	−
Age	−	−	−	+	−

drate concentration of the growing tissue while the other three (TEEM, SIMED and PT) assume that there is a saturating effect such that at high concentrations the growth rate will no longer continue to increase. This latter description agrees with results by Hunt and Loomis (1976) on *in vitro* cultures of tobacco callus. Their experiment showed a steep increase in growth rate at low sucrose concentration in the growth medium followed by a rapid levelling off of the growth rate at higher sucrose concentration. Their result is probably true for a wide range of organs and species and gives a general idea of the shape of the response curve. This is valuable information for growth modelling, but there is certainly still a long way to go before parameter values can be obtained that definitely fix the response curve. It would be of particular value to know whether or to which extent different organs follow different response curves.

Water

Everyone agrees that water has a great influence upon plant growth. Yet, the information actually describing how the water in the plant controls growth is very limited. This is not to say that little work has been done in this area – only that the kind of information available is not the kind of information needed when modelling growth. The problem is that water has a clearly recognizable effect upon extension growth and cell enlargement, while what is defined as growth in this article is irreversible incorporation of carbon into structural material, and generally it is the former processes that are studied. One study of the incorporation of carbon into cell walls of *Pinus sylvestris* was made by Whitmore and Zahner (1967) on excised tissues. They found a rapid decline in incorporation when the water potential of the surrounding media decreased to −6 bar, Thereafter the incorporation declined only slightly down to −30 bar.

The experiment by Whitmore and Zahner has been used to describe the effect of water upon growth in PT. CERES uses an exponentially decreasing growth rate between two plant water potentials, assuming no effect at higher water potentials and complete inhibition at lower ones. SIMED uses a very simplified approach by letting the controlling variable be the atmospheric water vapour deficit. The remaining two models do not use any water variable to regulate growth. Although in the description of TEEM some growth-regulating variables are said to depend upon the plant water potential, there is no mention of what this dependence should look like.

One major difficulty in attempting to include a water potential in the growth processes is the great differences in water potentials prevailing in a tree. A single value is therefore not a good description of the situations in all parts of the tree. In addition, we do not know whether different organs tolerate water stress differently. It is by no means obvious that a leaf should react to a water potential of say – 10 bars in the same way as fine roots should.

Nutrients

The literature abounds with fertilization experiments (e.g. Tamm, 1975). However, most of the reported fertilization experiments have not aimed at advancing our understanding but rather to obtain optimal fertilization regimes for the forest industry. The information necessary for understanding the role of nutrients in the regulation of growth derivable from those experiments is therefore limited. Also, what makes it difficult to analyze such experiments is the effect of the soil system and other vegetation. Typically, only 15–20 per cent of the applied fertilizer is recovered in the trees. Input–output analyses with fertilization doses as inputs and growth responses as outputs are therefore heavily obscured by the filtering effect of the soil system. More promising are the very well-controlled experiments by Ingestad (1977) which indicate that the growth rate can be described by the nutrient (N) amount available in the plant (nitrogen productivity). An interesting forest growth model has been developed based upon this idea (Ingestad *et al.*, 1981).

In view of what seems to be a fairly limited understanding of how the nutrients control growth it is perhaps not surprising to find that only one (PT) of the models attempts to explicitly include nutrients. In the other models it is either assumed that nutrients are available in optimal amounts (SIMED) or the question is passed in silence.

Temperature

Detailed information about the effects of temperature upon growth rates does not exist. However, for modelling purposes there are often three points that are fairly well-known: (i) a lower temperature below which growth ceases; (ii) an upper temperature above which growth ceases; (iii) an optimum temperature. Given these three points and assuming a continuous variation of growth rate with temperature, one can construct growth-temperature response curves. Although there is no unique solution to the problem of constructing the curve, as long as one is not dealing with pathological effects and one can assume the response curve to be smooth, the precise shape of the response curve will probably not matter too much for the growth response over a longer time period. Changes in the response curve due to acclimation can probably also be neglected in several cases. But, before any definite conclusion is drawn one had better perform sensitivity tests in the particular cases.

A possibly more serious problem with respect to growth responses to temperature is if the plant in some way integrates the temperature to form some kind of temperature-sum (e.g. Hari *et al.*, 1970) in which case small errors might add up. Such a function is also included in SIMED to describe maturation.

With respect to the five models under comparison one finds that the three (SIMED, SDF, and PT) with temperature dependent growth rates have defined them in approximately the same way and in all cases have about the same amount of information (i.e. quite little) for the construction of the response curves. The remaining two models have left the problem of temperature effects upon growth rates without comments.

Time (phenology)

The time of the year is explicitly included in the descriptions of the growth rates in two models (SIMED and PT). The main purpose of this has been to halt growth in the autumn. In the model this is presumed to occur via a shortening photoperiod. In the other three models growth rate decreases in the autumn only through the limiting effect of other factors, e.g. temperature or exhausted carbohydrate reserves.

Plant growth is generally started in the spring on a fixed date, with the exception of PT, where the growth period is initiated by a sufficiently high air temperature for a sufficiently long period.

These questions of the start and termination of growth are of course of the utmost importance in order to make correct predictions about the time course of the growth.

Statement VI: As has been demonstrated above, the understanding of the growth process *per se* is almost completely lacking. As long as this situation remains it is hard to see how mechanistic high-resolution growth models of the kind discussed in this article can make any progress. Until this has changed I think it will be necessary to resort to growth models where the growth process is treated in a very simplified manner.

Mortality

In growth models one cannot be content with only looking at what enters the plant, one has also to account for what leaves it. However, the problem of mortality is one of the most difficult ones, but can be of utmost importance in growth models. Ågren *et al.* (1980) found that in a young Scots pine stand 57% of the annual net photosynthetic production was dissipated in fine root death. It is easily recognized that under such circumstances even small errors in the fine root mortality can cause drastic effects on the carbon balance of the rest of the tree.

The treatment of mortality in the models is very scanty; one of the models (SIMED) does not even have any mortality. In the other models the mortality is generally assumed proportional to the amount of material present with the exception of the leaves that are forced to fall in the autumn. For models of species with several needle generations present simultaneously (e.g. PT) and where sometimes more than one generation can be shed in the same year a correct treatment of the mortality becomes of prime importance in simulations running over more than one year. For Scots pine, the contribution to the annual net photosynthetic production can be as much as 35–45% from the needles older than one year (e.g., production of stem wood amounts to 10% of the annual net photosynthetic production), and it is precisely these year-classes of needle that can stay on the tree or be shed in what looks like a random manner. However, it is obvious that an incorrect prediction of their mortality can upset the model results.

Statement VII: Along with growth processes this is the process about which the least is known. The problem is further complicated with trees in that much of the dead material remains within the living organism – the wood. Models without within-year dynamics can possibly neglect the very rapid and important turn-over of fine roots, which definitely would mean a simplification. An interesting mortality problem would be to investigate the consequences of the different mortality rates of leaves of different species and their implication for inter-specific competition.

Validation

In books teaching the use of systems analysis and simulation models, the step of validation is stressed as important. Yet, of our five models only one attempts a quantitative comparison between model output and measured data. Moreover, the comparison is restricted to one lumped state variable (stem and leaf dry matter) out of the six defined and to none of the ten flows. The other models only consider qualitative agreements between the model output and the observed system. Since the models contain 35–100 parameters the strength in these validation procedures is not overwhelming.

It is quite clear that the basic reason for not performing more rigid validation of the models is a lack of data. Several of the variables defined in the models correspond to properties that are not readily measurable, e.g. all properties pertaining to roots. In other cases, the concepts are not well defined, e.g. the total carbohydrate content of a tree. It is of course possible to define them as the amount of certain specified substances or the amounts extracted with certain specified techniques, but until then the exact nature of these state variables remains obscure.

An additional complication when setting up data bases for validation is that almost all measurements are destructive. Thus, in a time series of measurements these will never be done on the same system or only on a sample from the system. In either case a cer-

tain amount of error will be associated with each measurement, which will increase the possibilities of fitting several different model outputs to the same experimental data, thereby decreasing the possibilities of differentiating hypotheses in the model.

Discussion

As has been illustrated in the preceding section, the state-of-the-art in modelling tree growth is not very satisfactory. In my opinion there are several reasons for this situation.

(i) It is all too easy to, on paper, put down some boxes and connect them with arrows and then make some "reasonable" guesses about the values of these arrows. In less than a day a model of this kind can be in full swing on the computer. And, as has been discussed earlier, we are presently lacking good information about most of the processes in question and as long as we are lacking good data against which to validate the models there is no possibility of discriminating between different formulations. Therefore, as long as the models do not produce directly absurd outputs, "reasonable" formulations will survive. It takes a lot of courage to discard such a model as pure crap. Sometimes external (political) forces make it desirable to maintain the model.

(ii) There is an urge to make the model as "realistic" as possible by including all factors thought to be important. The model will therefore contain state variables for most of the different organs of the tree as well as the most important substances. However, as a consequence the models require a multitude of parameters, most of which are at best only known by their order of magnitude. It is then very difficult to relate the behaviour of the model to any particular formulation in the model and small changes of several of the parameters will generally produce any output desired.

(iii) Great expectations have been placed upon the models to provide quantitative results. In many cases the models have been constructed for the purpose of predictions. Under such circumstances it has been more interesting to get out several digit numbers rather than simple answers like a trend going up or down. This has been another force towards too complex, too all-encompassing models that actually cannot predict anything at all.

(iv) Inexperience. The technique of mathematical modelling has only quite recently been introduced from physics and technology for use in ecology and biology. The number of people with good training and knowledge in both mathematics and ecology/biology is therefore so far rather limited. It is, thus, not surprising that people experienced in the hard sciences were over-optimistic about the possibilities of introducing the same methodologies into new areas. Time has, however, taught us that the basic knowledge in ecology/biology is in several cases too limited to allow the indiscriminate use of simulation models.

The criticism presented so far may look rather harsh and possibly depressing. However, I am of the firm opinion that it is necessary unless one wants to perpetuate the mistakes made during the past decade. It is not my intention to condemn the utilization of simulation models but rather to point at what presently cannot be done with such models. The leading theme throughout this article is to show that in most cases we do know a little and only exceptionally do we have a good understanding of the processes relevant for modelling growth. What I strongly object to is the lumping of too much ignorance in the hope of getting out something sensible. I question whether such models as those discussed in this article are yet ripe for the scientific literature. They contain too many loose hypotheses and are too soft and flexible to be possible to put under some hard tests of falsification. I do not want to say that all work on similar models should be absolutely abandoned because working on such a model can teach the people involved quite a lot, but the result of such work should not be presented as more than a review of the level of understanding of the different processes.

Then, what do I think should be done in the future? I think that the use of mathematical models will become an imperative in much of

the future ecological research. However, it has to change its forms.

(i) One should not aim at constructing THE model. A complete and coherent picture of growth will not be the result of the work on one single model but will emerge from long hard work on several small models, each of which presents its partial solution. I would therefore strongly recommend that the work is concentrated upon what I called specific models in the Introduction.

(ii) Each model should not contain more than one part that is not well understood. For that part the model can be used as an instrument of testing different hypotheses.

(iii) There are several areas where essentially all the basic principles are known but where their consequences have not yet been deducted. Here I can think of problems like a better evaluation of the effect of the height of a tree upon its photosynthesis mediated via its water potential, or a better estimate of the light-damping in heterogeneous canopies.

(iv) Finally, one has to look more upon the real strength in the mathematical treatment of ecological/biological problems, which resides in the deduction. It is the possibilities of the mathematical analyses to disclose inconsistencies or dependencies in assumptions that really can advance the thinking about scientific problems. The mathematical models may no longer be regarded only as processors of data.

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Can We Model Xylem Production by Conifers?

E. D. Ford

Institute of Terrestial Ecology, Bush Estate, Midlothian EH26 0QB, U.K.

Abstract

At present models do not exist which can predict xylem production in relation to environmental conditions. The accuracy and distribution of measurements over the tree which are required for the development of such models is discussed.

Considerable emphasis is placed on the need to model xylem production at the tissue level and to predict cell production, enlargement and wall thickening. The control of these processes through carbohydrate supply and hormonal mechanisms is discussed in relation to how they might be modelled mathematically.

Introduction

The secondary cambium is the most important meristem of the tree for both economic and biological production. Height growth, and branch root extension lay the essential foundation on which the secondary cambium operates and, together with foliar production, they control the processes of photosynthesis and water and nutrient uptake. However if we wish to develop a physiologically based model which relates forest production to environmental influences then we would be quite justified in focusing our attention on the activity of the secondary cambium in xylem production and consider other processes only in so far as they have an influence on it. This is not how physiologically based studies of forest production have proceeded to date. There is a very marked contrast between the high degree of sophistication which has been built into models of the contributing processes, particularly of photosynthesis and water economy, and the rather simple models that we have of cambial activity.

The discrepancy reflects our comparative lack of understanding of the factors which control xylem production which in turn is the result of the difficulty of obtaining a measure of cambial activity appropriate to relate to environmental conditions and physiological processes. The problem of measurement has three components,

i. In common with measures of shoot and root extension and foliar production there are large spatial differences in cambial activity. If total cambial activity is to be related say to total photosynthesis at the stand level by constructing a carbon balance then these differences must be assessed accurately.

ii. The weather varies markedly over time periods of less than a day and models of photosynthesis and water loss from plants must take such short term variation into account if accurate integrations are to be obtained (Linder & Lohammar, 1981). To examine the effects which both the weather and physiological processes may have on cambial activity then we must be prepared to make assessments on the same time scale at which they vary. Unfortunately this cannot be achieved simply by accurate measurements of girth or radius. The quantity of material laid down must also be assessed in dry weight terms.

iii. Consideration of the relationship between radial growth and the deposition of dry weight leads to the analysis of the number of cells produced by the cambium, their expansion and wall thickening.

These measurement problems are of great importance and I wish to discuss how they might be approached for studies of xylem production in the forest. I also wish to consider some models for xylem production at the tissue level and if they are likely to provide an appropriate framework for studies attempting to integrate xylem production with other modelled processes. The physiolo-

gical mechanisms which underly the control of cell production, expansion and wall thickening are still a matter of debate, yet it is essential that we understand them rather better if we wish to be able to predict wood production and structure.

Spatial variation in xylem production

There is a well documented variation in xylem production between different positions on a tree. Thus for a dominant tree within a pole stage stand current ring width increases rapidly from the top downwards and reaches a maximum in the zone close to the base of the live crown. Ring width then decreases gradually towards the base of the trunk (Farrar, 1961). Generally the proportion of the ring occupied by spring wood decreases from the top downwards and therefore wood density increases.

At first sight these patterns of variation seem eminently tractable to mathematical analysis. General equations have been developed to describe tree form (Gray, 1956) but these are empirical with no basis in the mechanism of growth and so particular equations must be developed for special circumstances, e.g. to describe changes in tree form as a result of fertilization (Flewelling & Young, 1976) or growth of wide spacings (Grant, 1978). The difficulties encountered in modelling tree form are because the pattern of annual increment can vary markedly with tree age, between trees within a stand and significant variations can also occur in the distribution of ring increment in parallel with changes in weather (Duff & Nolan, 1953, 1957). Butt swelling, which alters the general shape of the tree height:ring increment curve is observed where there is a strong mechanical stimulus, e.g. tree sway in windy areas (Jacobs, 1954).

Variations in the annual pattern of wood increment to the tree trunk were extensively studied in the late nineteenth and early twentieth centuries. The three principal hypotheses as to the biological mechanisms that were advanced to account for observed patterns of increment and their variation between trees growing under different conditions have been reviewed by Larson (1963). The 'nutritional' theory describes variation in both ring width and the proportion of early to late wood in terms of the requirement of stem cross-sectional area for water conduction to fulfill transpiration requirements and which stimulates early wood formation. Once these have been met, the available resources for growth form latewood, considered as the 'strength' tissue. The 'water conduction' theory attributes variation in ring width as a necessary response to maintain a conduction path for water between roots and shoots as the amount of either varies. The 'mechanistic' theory describes wood production as the response to mechanical stimulus in the variation in ring width described as response to differences in either the vertical force of tree weight, perhaps increased in periods of wet snow, and the horizontal forces due to wind action.

Larson (1963) also reviewed the experimental work which these theories stimulated with an important conclusion which the modeller wishing to relate xylem production to physiological processes should consider.

The 'nutritional' hypothesis that wood production is limited by available substrate is generally insufficient to explain variation in ring width. The requirement of a stimulus to production has been demonstrated in a number of cases, and most dramatically in the case of mechanical stimuli. We cannot expect to model the control of xylem production entirely in terms of photosynthetic production.

Measurements to investigate xylem production in relation to environmental and physiological conditions

If we wish to study environmental influences on cambial activity then we must be prepared to analyse growth during a season. This is usually apparent to physiologists who have the objective of examining the large changes which can occur in photosynthetic rate, carbohydrate reserves and other processes. It is also apparent to dendroclimatologists who, in their search for an understanding of why ring widths vary, have increasingly sought ex-

planations in terms of weather variations within seasons (Fritts *et al.*, 1971). However, to provide a comprehensive picture of the factors which control the activity of the cambium in producing xylem then both the spatial variation of cambial activity within a season and the magnitude and frequency of environmental changes which can have an influence on production must be thoroughly examined.

In addition to the variation in total ring width between different parts of the tree which occur, and therefore in annual growth rates, differences have also been found in the periods when growth is made (Priestley, 1930). Generally diameter increments of branches and the upper trunk start earlier than that of the lower trunk. Diameter increment of suppressed trees starts later in the year and finishes earlier than that of dominant trees. Thus extrapolating the seasonal time course of xylem production from samples made at one point on the cambial surface can give an erroneous picture of the amount of material produced and certainly one which it would be wrong to use in isolation in any attempt to relate with photosynthetic production.

It is well documented that both photosynthetic rates and internal water potentials of trees vary markedly both between and within days. Their ranges of variation are sufficiently large and are influenced by variables which change both daily and over the course of the season that it is appropriate to define them in terms of their amplitudes and frequencies of change. The reason for this is perhaps most obvious for internal water potentials. Hsaio (1973) reviewed the effect of water potentials in arresting cell growth and wall extension. Both can be halted by reductions in tissue water potential between 0 and -5 bars whilst photosynthesis is not affected until reductions of -5 to -15 bars are experienced. There is considerable evidence that growth 'lost' can be recovered following relaxation of the potential. Thus the effect of internal water potentials on growth is likely to be a function of both their amplitude and duration. For trees in their natural environment the development of internal potentials largely follows the diurnal course of solar radiation. However, both size and duration of the potential reached can depend upon the size of the tree and on soil moisture levels which in turn are likely to be affected by environmental conditions over the preceding days.

All weather variables are strongly influenced by the diurnal radiation balance. If their effects on growth are to be studied directly in the natural environment then growth must be measured with sufficient accuracy and at a frequency which permits assessment of effects on a daily basis. These two requirements of high accuracy and frequency together with the need to make measurements at a number of positions on the tree suggest the use of linear variable displacement transducers. These devices comprise a small spring loaded plunger, one end of which is placed against the surface of the tree and offers a very small resistance to outward movement. The other end is contained within an electrical winding. The whole device can be fixed to the tree with an attachment which is remote from the point of measurement but yet ensures that the tree and instrument move together in a wind. As the tree expands or contracts the plunger is moved within the winding and a voltage change can be detected with an accuracy of $\pm$ 10 μ. The difficulty with this measurement system is that contractions and expansions in trunk, branches and roots occur which are related to the loss and uptake of water by the tree and its use for recording changes in tree girth *due to growth* depends upon the accuracy with which movements related to changes in internal water potential can be 'extracted' from the measured changes in voltage.

Despite some early optimism this has proved a difficult task (see Braekke & Kozlowski, 1975). There certainly seems to be hysteresis in the daily cycle of contraction and expansion so that the contraction which may be measured at a specific internal plant water potential as water is lost due to transpiration may not be fully regained when that internal plant water potential is reached again during the following period of net water uptake. This may be because water is withdrawn and replenished to different tissues

within the tree at different rates. Refinement of this measurement system to a point where radial 'growth' can be defined will require a detailed understanding in a quantitative model of what controls the movement of water into and out of the tree.

Radial growth is only one measure of xylem production. If we wish to relate xylem production to rates of photosynthesis and the carbohydrate economy of the tree then we must measure the total amount of material laid down and this requires estimation of wood density across the ring. This can be done by microscopic measurement and analysis of cell dimensions or by a microphotometric technique (Elliot & Brook, 1967) both of which require that accurate sections be cut and stained. Sampling and scanning for density at the end of a growth period after following a course of radial growth does not permit the reconstruction of a time course of cell wall increment because variations may occur in the time taken for cell walls to thicken. To follow the deposition of cell wall material during growth by taking repeated samples from the same region of the cambium may damage it and so influence further growth.

In an attempt to minimize the problem of damage due to repeated sampling the technique of inserting pins into the cambium has been developed. Cambial mother cells and xylem initials are killed over a small region and a few radial files of tracheids are 'frozen' at that particular stage of development but the rest of the cambium continues to develop.

It should be possible to chart the course of xylem production over a small zone of the cambium through combining accurate measurements of radial growth with a displacement transducer, a knowledge of those aspects of plant water relations which cause contraction and expansion of the radius, insertion of pins as markers of developmental sequences and the retrospective sectioning and densiometric survey along radial files of tracheids where the pins were inserted. However the intensity of effort required to do this would make its application on a sufficient scale to survey spatial variation in xylem production very difficult.

Models of xylem production

Three models of xylem production and development in conifers have been proposed. None are structured to simulate the effects of environmental or physiological conditions on xylem production directly but each contains important assumptions or provides valuable results which must be carefully considered if this is to be done.

Wilson and Howard (1968) simulated the annual production of a single radial file of tracheids. They considered that three independent biological processes were involved; cell division, cell enlargement and cell wall thickening. 14 parameters, summarized in Table 1, were used to simulate the control of these processes in the production of xylem and the determination of its final structure. By selecting new values for these parameters in successive 5 day periods they were able to simulate the growth and development of a radial file of tracheids which at the end of a 'year' had the same mean values of cell numbers and showed similar changes in cell diameter and wall thickness as observed radial files.

Howard and Wilson (1972) appreciated that there is a variation between parallel radial

Table 1. Parameters used by the model of Wilson and Howard (1968) in simulating the annual production of a radial file of tracheids.

Cell division	Cell enlargement	Wall thickening
Rate of radial cell enlargement of mother cells	Size at which cells enter this phase	Size at which cells enter this zone
Rates of radial and length growth of cambial mother cell	Rate of enlargement	Rate of wall thickening
Size at which a mother cell divides		Maximum wall size when cell is mature
Size at which cambial initial divides		

files of tracheids. They modified their deterministic model (Wilson & Howard, 1968) so that the 14 parameters were each specified with a standard deviation which corresponded to the level of variation observed between cells. They found that repeated simulations where parameter values were permitted to vary with the specified errors gave radial files of different total lengths and concluded that it would be necessary to include some degree of interaction between files to constrain their development in order to model a segment of a complete ring. An alternative explanation is that the error terms should not be applied uniformly to all parameters.

Wilson (1973) appreciated that specifying xylem production in terms of rates of cell division, enlargement or wall thickening begged the question of how these rates were controlled. He developed a model whereby cell division and enlargement, but not wall thickening, which he deliberately excluded from consideration, were controlled by the concentration of an unspecified substance within the cell and this in turn was controlled by its rate of diffusion from the phloem to the dividing or enlarging cell. Again the total annual production of xylem and its final structure of cell radial diameters were simulated to correspond with observed rings but this time by varying only two inputs through the 'year'. These were the concentration of the unknown growth substance at the phloem and a factor which specified the slope of a linear relationship between concentration of the substance within the cell and the relative growth rate of expansion for that cell. Seven other parameters such as a diffusion coefficient and minimum concentrations at which either division or enlargement proceeded were fixed as constant. An effective transition of cells from the division to the enlargement zone was maintained simply by limiting division to cells which had grown to a certain size yet which still contained a high concentration of the growth substance.

Towards a model simulating environmental effects on xylem growth

Denne and Dodds (1981) have described the complex set of plant physiological processes which contribute to or influence xylem production and structure. Many environmental factors have been reported to influence this growth. Indeed we might expect that any environmental factor which can alter the rate of a component process might come to have a controlling influence on the rate and the structure of xylem production if conditions were such that this process limits the rate of production.

Denne and Dodds (1981) pointed out that variation in a single environmental factor, e.g. temperature, may have an effect on a number of the processes contributing to growth. Furthermore, the effects of environmental variation may change depending either upon the previous state of the plant or upon variation in the levels or conditions of other factors and they reviewed work where similar variation in a single factor had apparently contradictory results. Because of this complexity it is most likely that attempts to equate environmental variation directly with variation in amount of xylem produced or its structure will have no more success than previous attempts to describe variation in the thickness of the annual ring over the tree as the operation of one simply stated mechanism. If we are to build a model of environmental influence on xylem production then we must be prepared to specify this influence through the intermediate pathways of the growth process. The problem of modelling then becomes one of producing mathematical formulations of the relationships between environment and growth which can be tested by experiment. Our present requirement is to specify those parts of the network leading to xylem production which we can measure, and establish relationships between them. It is unfortunate that the models of Wilson and Howard (1968), Howard and Wilson (1972) and Wilson (1973) are not in such terms and so cannot act as a basis for progressive study.

Environmental factors have frequently

been classified as having direct or indirect effects on xylem production, e.g. Denne and Dodds (1981), Worrall (1980). A direct effect is considered to operate on the growth process at the level of the cambium or on the differentiating cells whilst an indirect effect might occur through an effect on substrate availability or on the balance of growth regulators (Figure 1). The classification of factors as direct or indirect is not particularly helpful to the model builder, as Denne and Dodds have pointed out, a single environmental factor may influence all three processes. However, the classification is a recognition that in order to reconcile some of the very different results which have been obtained then xylem production must be considered at three component processes. I suggest that our current task is to describe in mathematical terms, the process of *i.* cell development at the tissue level, *ii.* limits to growth set by the rate of substrate supply and *iii.* control through plant growth substances, and that this should be done in such a way that their inter-relationships might be examined.

The relationship between cell division, expansion and wall thickening in developing tissue

A fundamental assumption of the models outlined above is that cell enlargement and cell wall thickening are independent. This hypothesis has frequently been advanced from work where the annual course of xylem growth and development has been studied. Thus Wodzicki (1971) described the transition in production from large narrow-walled cells in spring to the small thick-walled cells of latewood in terms of an increase in both the duration of cells in the thickening zone and in their rate of thickening and a parallel decrease in duration spent in the cell expansion zone and in the rate of expansion.

An alternative hypothesis to explain the transition from early to latewood has been advanced by Bethel (1964). He obtained similar patterns of cell diameters and cell wall thickness along radial files of tracheids to those described by Wodzicki. However when Bethel calculated cell wall area per cell rather than cell wall thickness he found a generally constant value across the ring and certainly no clear change which separated early from latewood although small regular variations were apparent. Bethel proposed that the potential for cell wall volume development is established at the time of cell division, that this is largely constant along a single radial file and is independent of the enlargement which the cell subsequently undergoes.

Both Wodzicki (1971) and Bethel (1964) analysed comparatively slow growing wood. The Scots pine ring studied by Wodzicki was at the base of a 70-year-old tree and produced

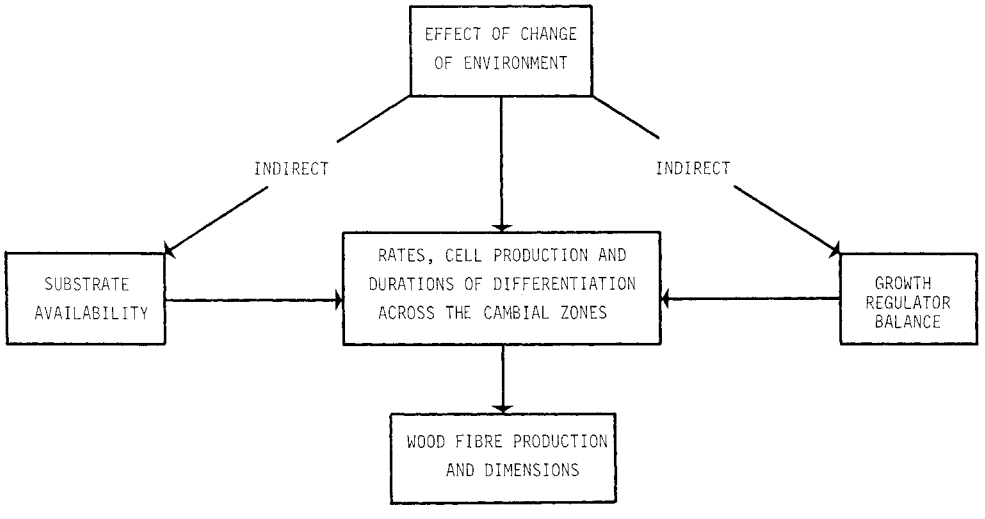

Figure 1. Scheme for the control of xylem production. Modified from Denne & Dodds (1981).

only 34 cells whilst Bethel studied two annual rings of *Abies grandis* where 18 and 22 cells had been produced. In the early wood of much faster growing timber of *Picea sitchensis* Ford *et al.* (1978) reported that large diameter cells also had thicker walls to the extent that denser wood was produced and suggested a link between the amount of time that individual cells spent in the expansion and thickening zones. This work was based on sampling twice daily at the base of the live crown where 60 cells were produced in 12 days.

From work with their stochastic model Howard and Wilson (1972) pointed to the need to consider possible interactions between neighbouring files. This requirement could be extended to models of growth dependent on a diffusion process. Whilst Wilson (1973) considered the source of growth substance as the phloem and diffusion to be along the radial files of cells themselves, perhaps lateral diffusion from ray cells should also be considered. The results of Bannan (1951, 1965) have shown that the fusiform cambial initials which are not close to rays have the greatest chance of being lost from the cambium by the differentiation of all their products whilst Carmi *et al.* (1972) demonstrated that both the number of rays and the proportion of tangential area which they occupied can increase when wood is stimulated to fast growth along a laterally restrained channel. Some aspects of the fluctuation in amount and dispersion of ray tissue between and within species and in relation to growth rate have been discussed by Catesson (1980).

I suggest that our understanding of xylem production as the growth and development of a tissue is not sufficiently advanced to permit us to model it in such a way that might permit interfacing with either substrate or hormonal based models of the influences of environmental effects. There are two important problems:

a) Are cell division, expansion and wall thickening completely independent processes? Or can some of the apparent differences in their control be resolved simply by considering other quantities as Bethel has suggested? Certainly if we wish to consider the diffusion of material to the developing xylem then total density of wall formation is likely to be an important parameter to measure.

b) Does the tissue change in character as its rate of growth alters? Again if we are to consider a growth model incorporating diffusion processes then we should investigate possible changes in ray density and size and possible differences in the probability or death of new radial files or in cell growth rates of established ones in relation to the proximity of cambial cells to radial files of tracheids.

Limits to growth set by the rate of supply of substrate

At first consideration it would seem a reasonable objective to attempt to relate xylem production expressed in dry weight to photosynthetic rate assuming, that is, that plants were used of a size where both variables could be estimated accurately. However developing a mathematical relationship between photosynthesis and growth is likely to be complicated by the operation of a number of intermediate physiological mechanisms.

Photosynthetic rates themselves are influenced by the internal conditions of the plants and not solely by external physical or chemical factors. Smith (1976) demonstrated that when seedlings of *Picea sitchensis* were exposed to changes in night temperature or in the quantity of light they received, then changes in photosynthetic efficiency occurred which tended to minimize treatment effects on absolute growth. He also showed through a ^{14}C labelling technique that in plants which had been changed to unfavourable environment that incorporation into turnover materials increased over the controls whilst that into storage materials and growth decreased. In plants moved to more favourable environments increased incorporation into turnover materials was also observed although in this case there was less movement of the label around the plant and Smith attributed this to an overloading of the substrate transportation and utilization system.

In seedlings then, photosynthetic rates may be controlled by substrate levels. This

hypothesis is likely to be difficult to test in large trees. However the suggestion has been made by Wargo (1979) that radial growth is related to the levels of carbohydrate stored. He suggested that in sugar maple substantial storage of carbohydrate precedes radial growth of roots whereas in shoot radial growth precedes or coincides with carbohydrate storage and we need to examine the possibility that this also occurs in conifers.

A principal requirement is to investigate the flexibility of the supply mechanism either from storage or through changes in photosynthetic efficiency. Such a process must be specified as a feedback loop, or perhaps a network of such loops. It is important to stress that the analysis of feedback systems must be investigated by exposing plants to change, this is the classic type of experiment of systems analysis (Milsum, 1966). What is required is to determine the scale and frequency of environmental change which produces specific changes in the various processes of carbohydrate supply. Models have been written which specify the production, supply and utilization of photosynthate as a network of differential equations (Ledig, 1969; Promnitz, 1975). Whilst these may be 'satisfactorily tested' under steady state conditions, work on similar models with tomato (Thornley & Hurd, 1974) suggest that difficulties may be encountered when plants are exposed to changes in the environment (Ford & Milne, 1981).

I suggest that an attempt to specify the relationship between photosynthetic rate and growth must take into account the intermediate stages of carbohydrate metabolism and that this may require the analysis of feedback mechanisms. However, specifying growth in these terms has the advantage that such models of substrate supply might be directly linked to models for the diffusion of resources into the cambium and xylem tissue from the phloem.

The control of xylem production and structure by plant growth substances

Modelling the influence of plant growth substances on xylem production and development presents a most difficult task. The wave of cambial activity which proceeds basipetally from the tree apex in spring has been described on a number of occasions (e.g. Priestley, 1930) and attributed to production by expanding buds or growing shoots of plants growth substance(s) (Wareing *et al.*, 1964; Larson, 1964). Frequently this wave is very regular and it certainly may be possible to describe its progress in time by descriptive equations for a set of well defined circumstances. However to relate this wave of activity to fluctuations in plant growth substances requires a certainty of theory of the mechanism of action and an accuracy of measurement of growth substances, both of which we lack. For example, Digby and Wareing (1966) demonstrated that important interactions could occur between indole-acetic acid (IAA) and gibberellic acid (GA) in the actions on the development of the cambium, but the full range of possible interactions between growth substances, perhaps originating from different regions of the plant has not been explored.

It is particularly difficult to exclude gradients observed *in situ* from the possibility of having an influence on xylem production. Thus Wareing (1980) has pointed out that all the major classes of endogenous growth substance have been reported present in root extracts and xylem exudates and phloem sap, suggesting their upward movement, but that their role on growth cannot be fully assessed. All experimental work into the role of plant growth substances is made difficult by the problems of measurement of endogenous levels, particularly in conifers. Concentrations are small, 1 part in 10^6, and multistep analytical procedures are necessary for their isolation (Crozier, 1980) which in itself can present serious difficulties.

A complex model for the control of cambial activity by auxin has been summarized by Wodzicki (1980). Basipetal transport was reported to vary in a wave line pattern with a wavelength of 2–4 cm which is several times the length of the cells of the cambium. The amplitude of the wave of auxin could be affected by application of other plant growth substances; IAA increased the amplitude

whilst abscisic acid decreased it. Wodzicki reported that these modulations were propagated basipetally along the wave systems several times faster than reported rates of transfer of IAA itself and invoked the involvement of a supracellular system to explain this. The importance of the wave–like system is in maintaining the orientation of divisions within the cambium. The general interest to the modeller of the transmission of the auxin stimulus in a wave–like pattern is that it opens the possibility of mathematical expression by wave length and amplitude which has many parallels in other biological systems which have been modelled (Milsum, 1966).

Conclusions

At present we lack both theory and measurement systems to write testable, functionally based models of xylem production and differentiation. This is so whether we consider the development of successive rings of a forest grown tree, the annual development of a single ring system or growth and development at the tissue level.

An understanding at the tissue level is a first priority from which understanding at the whole tree level is likely to proceed. However, progress towards this is most likely to be made for seedlings which can easily be subjected to fluctuating conditions and where more of the component processes can be accurately measured than for large trees. Exposure to fluctuating conditions are particularly necessary experimental treatments if the flexibility of the plant system in creating and mobilizing the resources for growth is to be explored in relation to xylem production.

I have suggested that when considering the development of the xylem tissue three aspects in particular require study: (*i*) the spatial relationship between the parallel developing radial files of tracheids and the rays, (*ii*) factors which control the supply of substrate to the growing points, and (*iii*) hormonal control. It is quite possible that the most effective models for these sub-systems are not mathematically compatible. The birth, development and death of radial files and their relation with supporting rays might be modelled as a branching process; substrate supply and utilization as a diffusion process and, if the theory advanced by Wodzicki of auxin advancing in a wave–like front is found to have generality, then time series modelling would possibly be appropriate. Where such different mathematical techniques have been used then the unification of process based models is more likely to proceed as an advance in understanding than as a single mathematical structure.

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Modelling of the Dry Matter Accumulation in Plants by Means of Asymptotic (logistic) and Exponential Functions

W. Żelawski

Department of Plant Physiology, Institute of Plant Biology, Warsaw Agricultural University, 02-528 Warsaw, Poland.

Abstract

Applicability of asymptotic (logistic) functions, commonly applied in growth analysis of plants, is discussed and the emphasis put upon their formalistic, non-explanatory, character. A new growth model, which is a modification of the exponential function, is proposed. An attempt at explaining the essentially sigmoidal shape of the growth curve, and the possible deviations from it, is based on an equation containing parameters which may have certain biological or physical importance. It seems that efforts towards formulation of an explanatory model of plant dry matter accumulation could take advantage of the fact that all external or internal factors limiting growth act through modifications of photosynthesis or related processes so the adequate parameter (or variable) of the function can be an integrating measure of these effects.

Asymptotic (logistic) models of growth in plants

The concept of the "grand period of growth" was introduced into plant physiology as early as in 1873 (Sachs, 1882). Later on it was extended to various kinds of growth, including dry matter accumulation, despite the fact that Sachs made only elongation measurements with organs of limited size increment. However, when growth is considered as the weight gain, related to incorporation of organic substances into the permanent structures of plant body, the Sachs concept does not seem to be fully adequate. It implies that growth rate decreases gradually when the final size is approached whereas accumulation of dry matter in plants, being related to photosynthetic activity of assimilatory organs, ceases rather abruptly at the last stage of senescence when the leaves are dying off. In this connection one could say that in dry matter accumulation the "grand period of growth" lasts until the very end of plant life.

As a consequence of the idea of the "grand period", functions with asymptotic value of final size were extensively applied in the quantitative analysis of plant growth and dry matter accumulation. These functions, often called "logistic", are generalizations of the simple logistic, or autocatalytic function which has been widely used in studies of population dynamics as well as in the growth analysis of animals (see reviews: Prodan, 1961; Fiedler & Thomasius, 1967; Richards, 1969; Erickson, 1976; Karmanova, 1967; Walter & Lamprecht, 1976; Turner *et al.*, 1976; Żelawski & Lech, 1980).

When this function is to be fitted to experimental data, for descriptive or computational purposes only, then any mathematical formula, including polynomials of various degree, can be useful, provided it is flexible enough and tractable with approximation techniques. However, these purely formalistic functions cannot help us to understand how growth proceeds in its relation to definable internal and external factors. Therefore, a search for biological interpretation of parameters of these functions, as well as using them for predictions, appears to be an abortive effort. Unfortunately the asymptotic (logistic) models are sometimes treated as adequate theories of growth, which leads to confusion, even in textbooks.

One of the difficulties encountered when the logistic model is fitted to experimental data consists in estimating the asymptotic final value to which plant weight would eventually approach as the growth proceeds. This

value must be arbitrarily chosen although it is often interpreted to express an inherent growth potentiality which is simultaneously affected by environmental factors. However, the two components of the asymptotic final size are not distinguishable within the logistic model (Richards, 1969; Barnes, 1977). Its assumption implies growth rate to be predetermined by a "maximum attainable size" which, however, may never be accomplished if environmental effects interfere. Parameters of the logistic function are interrelated with each other and do not permit any meaningful interpretation. From this point of view the logistic model is by no means a better description of growth than polynomials of various degree, numerous parameters of which are also biologically meaningsless; but at least, flexibility of polynomials is sometimes of certain advantage when only the best fit, for descriptive purposes, is needed.

From among the diversity of asymptotic functions the comprehensive one of Richards (1959) seems to approximate plant growth most realistically, since it permits descriptions of situations where the inflexion point occurs at later stages of growth. However, Richards (1969) himself was aware of the indeterminability of the asymptotic constant and gave a critical review of its interpretation. The most recent generalizations, which contain a kind of "generic function" with additional parameters (Turner *et al.*, 1976), or take into account the "population density factor" (Barnes, 1977), do not overcome the difficulties related to the assumption of an asymptotic model either; Richards' function is still considered as the best approach to growth analysis of plants (Venus & Causton, 1979).

There is, in fact, a considerable variation in the final weights of various plants but these are caused by individual differences in growth rates and in reaction to environmental constraints. The attainment of the final weight does not imply any exhaustion of growth potentiality. Due to continuously occurring photosynthetic production the processes of growth and dry matter accumulation remain as they were throughout the whole life of the plant (or growing season). As long as there are active assimilatory organs, on one hand, and meristematic tissues, on the other, the total weight of a plant must still increase. Moreover, because photosynthetic activity still continues, even when visible symptoms of senescence appear in assimilatory organs, the accumulation of dry matter does not cease and, in fact, does not slow down until the very end of the plant's active life. Removal of floral initials of monocarpic plants may prolong vegetative growth and consequently increase both the final size and the life span of a specimen (see reviews: Leopold, 1961; Sax, 1962; Wangermann, 1965; Żelawski, 1980). Growth of a plant is, then, theoretically unlimited, as already de Candolle (1883) speculated, and only conditions limiting photosynthesis, like e.g. deterioration of environmental factors, competition of neighbours, damage or natural senescence of assimilatory organs, etc. may bring about cessation of dry matter accumulation.

From this point of view there is no reason to ascribe biological meaning to the asymptotic value of final size, or consequently to any other parameter of the logistic model of growth; functions of this type should be treated as purely formalistic ones.

Exponential model of growth in plants

Attempts at formulating an explanatory model of dry matter accumulation in plants should take into account the primarily exponential character of growth and the progressive deviation from it. This deviation could be related to the gradually increasing demand for photosynthetic products that occurs in the growing regions other than those responsible for producing new leaves. If only assimilatory organs were produced, as in a population of unicellular algae or if a constant fraction of equally active photosynthetic tissue were maintained in a growing plant, then growth should always be exponential (Richards, 1969). But in the growing plant this is usually not the case and the fraction of non-assimilatory tissues gradually, though not always uniformly, increases. Thus, the model should contain a parameter, related to production

and distribution of photosynthetic products, that would increasingly affect the growth exponent of the exponential function as time proceeds. Such a parameter could be an integrating measure of environmental effect because all external factors act upon dry matter accumulation through modifications of photosynthesis and related processes.

Blackman (1919) was the first to introduce the exponential law of growth, $W = W_0 e^{rt}$, into the plant physiology although the Malthus idea of "unlimited" growth is almost 200 years old. Biologists, however, have always been aware that growth of any organism, in fact, is limited, so the exponential law is applicable to its early stages only. The relative growth rate, which by exponential growth is equal to the growth exponent "r", later exhibits an ontogenetic drift which is usually modelled by manipulation with the ratio of actual to final asymptotic (or *vice versa*) sizes of an organism (see Richards, 1969; Kvet *et al.*, 1971; Żelawski & Lech, 1980).

There is one function which normalizes growth with the maximum time during which the maximum size is achieved instead of the maximum (asymptotic) size itself (Zotina & Zotin, 1967, 1973). The function is not flexible enough to be directly applied to plant material but the idea of maximum time seemed to be useful in further development of the model (Żelawski & Lech, 1979). By intro-

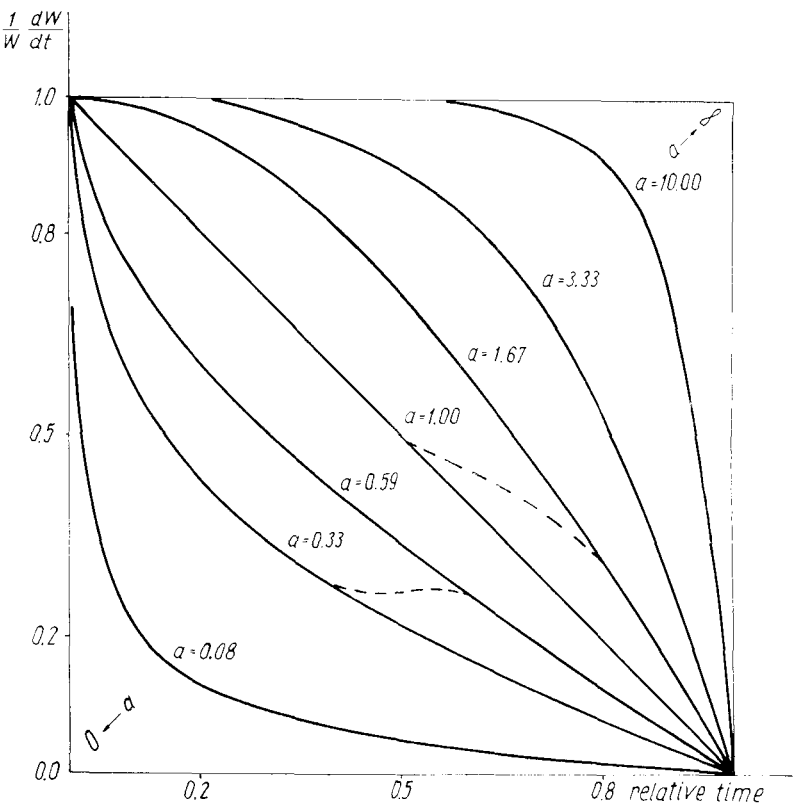

Figure 1. – Differential equation

$$\frac{1}{W}\ \frac{dW}{dt} = r\ \left[1 - \left(\frac{t}{t_m}\right)^a\right]$$

with different values of parameter "a"; broken lines portray exemplary changes in the course of relative growth rate when "a" increases from one to another value (sudden improvement of photosynthetic products' supply).

ducing a new parameter "a", the relative growth rate could be modified as follows:

$$\frac{1}{W}\frac{dW}{dt} = r \left[1 - \left(\frac{t}{t_m}\right)^a\right]$$

Then the integral form of this function is:

$$W = W_0 \exp\left\{rt\left[1 - \frac{1}{1+a}\left(\frac{t}{t_m}\right)^a\right]\right\}$$

In the differential form the expression $\left(\frac{t}{t_m}\right)^a$, and in the integral form the expression $\frac{1}{1+a}\left(\frac{t}{t_m}\right)^a$, vary between 0 and 1 by which growth either approaches exponential form $a \to \infty$ (almost no constraints) or can be modelled to various forms of the sigmoid curve $a \to 0$ (deteriorating conditions) and $a = 0$ (no conditions to grow). The parameter "a" exerts an increasing effect upon the relative

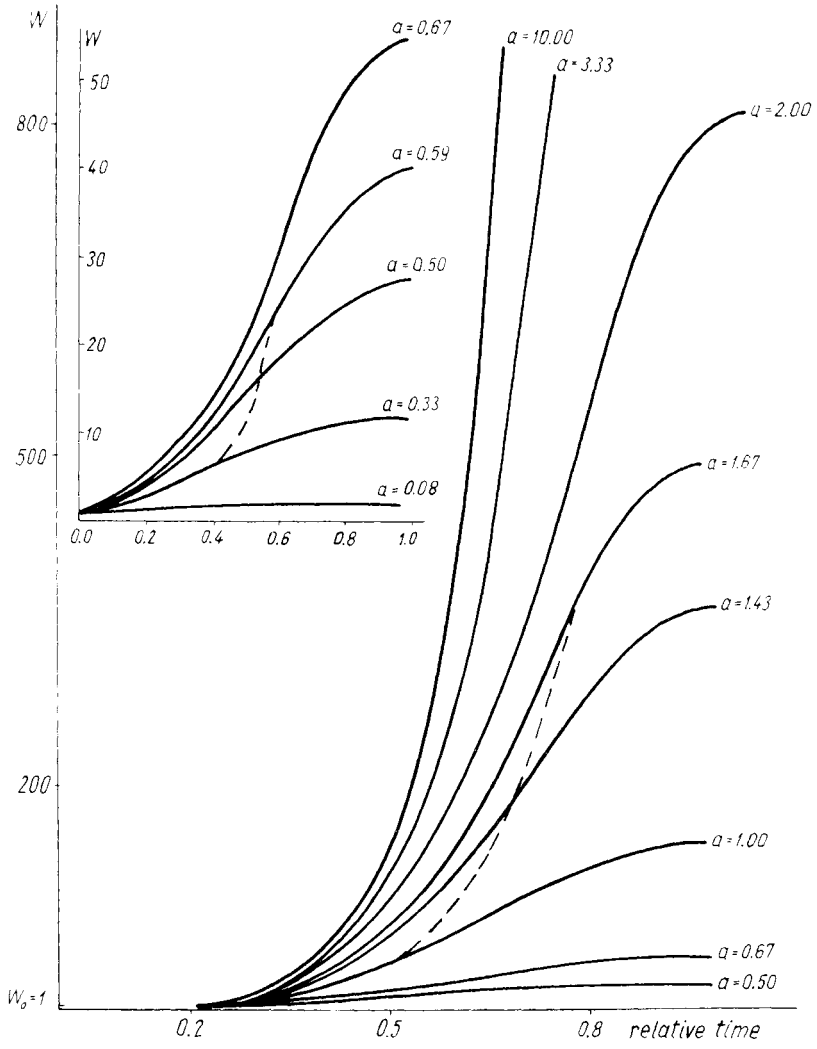

Figure 2. – Growth function

$$W = W_0 \exp\left\{rt\left[1 - \frac{1}{1+a}\left(\frac{t}{t_m}\right)^a\right]\right\}$$

at varying values of parameter "a" ($W_0 = 1$, $r = 1$); broken lines portray exemplary changes in the course of dry matter accumulation when "a" increases from one to another value (sudden improvement of photosynthetic products supply).

growth rate and upon the value of the function as time proceeds and the ratio $\left(\frac{t}{t_m}\right)$ approaches unity (Figures 1 and 2). The function is quite flexible: the earlier its inflexion point occurs in the growing period the lower the parameter "a". When "a" is assumed constant the function may be treated as the first approximation of the growth process concerned. However, besides situations with a constant parameter "a", the growth course can also be described while "a" is a variable (Figures 1 and 2, the examples are marked by broken lines); although no simple form of integrated equation is derivable when "a" is a function of time the model can still be useful when numerical procedures are available.

Interpretation of parameters in the proposed growth function

It is not easy to formulate a growth model that would have a predictive power because the time course of factors affecting dry matter production and distribution, as well as the total period during which the weight increment may take place, are difficult to predict from the *a priori* data. It seems, however, that a mathematical description made *a posteriori* could not only provide a short record of experimental data, as other functions do, but also help better to understand how the growth proceeded as a result of the interaction of internal and environmental effects. If certain physical or biological quantities are attributed to the parameters of the function then the model becomes an explanatory one. In fact, the model presented above is an attempt to explain the essentially sigmoidal shape of the growth curve, and the possible deviations from it, using a non-formalistic approach.

In the proposed function the initial weight (W_0) together with the initial (maximum) relative growth rate (r) define plant potentiality to grow. The power parameter (a) acting on the relative time $(\frac{t}{t_m})$ combines both the internal and the external photosynthetic constraints, whereas the maximum time (t_0) which normalizes the time variable (t) is rather a function of physical (meteorological) conditions.

The description *a posteriori* makes sense only when the experimental data are representative enough to be treated as a good approximation of the true values of the function. If this is the case, instead of fitting curves, an action of constraints can be estimated throughout the whole period of growth. Translation of particular environmental effects into the definite values of parameter "a" would make the proposed model useful in growth simulation studies.

One could argue that the assumption of the maximum time (t_m) in the new function is of no advantage over the asymptotic final size in the logistic model because it too is not predictable. However, certain superiority of the new approach is seen when one compares the adequate formulas for calculation of the maximum plant weight:

$$A = \frac{W_0}{(1-b)^{\frac{1}{1-k}}}; \quad W = W_0 \exp\left\{\frac{r\,t_m}{1+\frac{1}{a}}\right\}$$

In the first case, maximum weight (A) is a never attainable constant value resulting from the shape of the growth curve and independent of the most important characteristic, i.e., the growth exponent "r"; it is interrelated with some indefinable parameters of the comprehensive, logistic function. In the second case, maximum weight (W_m) is a really attainable value. It is a function of: 1) initial weight (W_0), 2) initial (exponential) relative growth rate (r), 3) maximum time, i.e. the length of the growing period (t_m), and 4) photosynthetic constraints (a). They all affect the maximum weight in such a way that their increase also increases the weight.

On the other hand the maximum time, which under particular conditions can be considered either as the length of the growing season or as the total life-span, equals:

$$t_m = \frac{t}{\left(1-\frac{R}{r}\right)^{\frac{1}{a}}}$$

where: R is a particular value of the relative

growth rate, i.e. $\frac{1}{W}\ \frac{dW}{dt}$ in the differential equation, for the given time moment (t). The maximum time increases under conditions limiting dry matter accumulation (low parameter "a") and also when the initial relative growth rate (growth exponent "r") is low. Trees growing under severe conditions, e.g., at the northern or upper timberline, are good illustrations of this thesis.

The maximum time represents the moment when dry matter accumulation stops either as a result of the deteriorating conditions of photosynthesis at the end of a growing season, or due to extinction of the photosynthetic activity at the end of life. In the first case, t_m is a function of meteorological conditions and in the second one, it is also a function of other physical limitations which preclude further photosynthesis. The predictive value of the above formula is, however, limited because "t_m" is related to "a" and "a" may not be constant within the future period, between t and t_m. From the definition of the presented model it follows that the function cannot be used for estimating "a" unless "t_m" is known, or *vice versa*.

Experimental data of a real course of growth can be used to calculate the value of parameter "a" for each time interval of the growing period. Computation is made by use of the interactive procedure when applying the formula:

$$a = \frac{\left(\frac{t}{t_m}\right)^a}{1 - \frac{\ln W - \ln W_0}{rt}} - 1$$

The value of parameter "a" can be a measure of the availability of carbohydrate reserves which provide materials for new growth of assimilatory organs. The simple model of carbohydrate-limited growth is given by Hunt and Loomis (1976) for tobacco callus. Ericsson (1979) has shown that in Scots pine needles the pull of phytosynthetic products seasonally varies and during the period preceding new shoot growth the level of carbohydrate reserves may even exceed 25% of the dry weight. It would be interesting to relate changes in the availability of photosynthetic products with the rates of an accumulation of organic substance in the permanent structures of an plant organism, by which the parameter "a" could become a measurable value.

McKinion *et al.* (1975) have built the system of equations in which the decrease in photosynthetic rate caused a decline in the availability of carbohydrate reserves and consequently brought about a change in initially exponential or linear courses of dry matter accumulation, so the curve became sigmoidal at later stages of growth. It seems quite rational then to try to relate the typical shape of the growth curve to the action of photosynthetic constraints.

Various conditions that limit dry matter accumulation act, either directly or indirectly, through photosynthesis or related processes. Constant value of the parameter "a" expresses the same action of photosynthetic constraints throughout the whole period of growth; as the result of continuous augmentation of plant body the same level of availability of photosynthetic products throughout the growing period brings about more or less sudden extinction of dry matter accumulation at the latest stage. Therefore a function with the constant parameter "a" portrays a typical sigmoidal growth curve. A real curve may, however, assume almost any, though always ascending, shape and then the parameter "a" should be considered as a variable changing gradually or suddenly, e.g. after irrigation, fertilization, impact on insects, drought, frost, etc.

Old trees in the last phase of their life may provide an example of strengthening internal limitations where positive feedback, between water transport, photosynthetic activity, and distribution of photosynthetic products, causes shortage of materials for further wood increment and brings about cessation of growth. After a prolonged phase of non-limited, close to exponential or linear growth, trees exhibit a rather short phase of extinction, leading to death. On the other hand, from forest mensuration data it is known that even heavily stressed trees, which are being eliminated by the process of self-thinning, do not cease their volume increment gradually but after the phase of intensive growth they

enter only a short period of decease. This means that the supply of photosynthetic products begins to limit further growth only when the increasing closure of the canopy causes drastic deterioration of illumination in the crown. The very well known fact that trees deprived of a competitive neighbourhood are able to resume growth with a new energy, resembling early phases of life, can also be explained on the basis of the presented approach. On cross-sections of old trees it is often possible to recognize many periods of suppression and renewal of growth.

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Modelling of the Functioning of a Tree in a Stand

P. Hari & S. Kellomäki

Department of Silviculture, University of Helsinki, SF-00170 Helsinki, Finland

Abstract

One approach to the analysis of the functioning of a forest is presented. Four postulates are introduced which are considered to characterize the most essential features of forest development. The general structure of models for an individual tree is discussed. It is suggested that tree models should utilize the results of evolutionary theory, according to which the functioning of plants gradually adapts to the environment. This enables certain parameters to be determined by means of mathematical optimization techniques.

Study approach

Ecological research has produced a large amount of apparently unconnected observations. These results have not yet been systemized. For this reason, there are several alternative ways of characterising the functioning of a tree in a forest. The following postulates were chosen as the most important properties:

1. There is great spatial and temporal variation in the functioning of a tree and in environmental factors.
2. The trees regulate their own functioning.
3. The trees interact with each other by modifying the environmental factors.
4. Evolution has optimized the functioning and the structure of the trees in their own characteristic environment, and they have adapted to it within the limitations imposed by their present structure.

The structure of models describing the functioning of a tree in a forest was developed on the basis of the above postulates.

The dynamics of metabolic processes

Both temporal and spatial variation in the metabolic rates are very pronounced (postulate 1). This variation is largely generated by the variation in the environment. Pure environmental variables are, however, insufficient for analysing the variation of metabolic rates, since trees regulate their own functioning (postulate 2). Self-regulation is introduced into the models by means of the internal state, S, of the plant. The biochemical regulation of plants represents a complex system which could be modelled using the activities of the individual chemical components, but its great complexity renders it nearly impossible. The internal state S introduces the total effect of the biochemical regulation system of the tree into the model. Let vector m(X, t) denote the rates of the metabolic processes in a unit mass of plant at point X and moment t. These rates are largely determined by the environmental factors Y(X, t) at point X and moment t, by the internal state of the plant and by the location, i.e.

$$m(X, t) = f_1(Y(X, t), X, S(t, X)), \quad (1)$$

where f_1 is a vector of functions, the components of which are process specific. The internal state S is also a vector, which is not constant. Let vector s denote the rate of change of the internal state. It is determined by the environment and the internal state, i.e.

$$s(t, X) = f_2(Y(X, t), S(t)). \quad (2)$$

Equation (2) allows determination of the internal state by integration if its value is known at some instant, t_0, and if the environmental conditions are known after the instant t_0 (and if the function f_2 is sufficiently regular). Let m_{pl} denote the rates of metabolic process in a tree and the density of its leaves. The rates of metabolic processes in a tree m_{pl}

are obtained by integration, over space, of the rates at points

$$m_{pl}(t) = \int_V (X)\, m(X, t)\, dV, \qquad (3)$$

where V is the volume of the plant. The dependence of a metabolic process on environmental factors is usually nonlinear. This is why the integration in Equation (3) cannot be substituted by averaging. The experimental work based on Equation (1) is demonstrated in Figures 1 and 2 and the integration over space (cf. Equation 3) in Figure 3. The application of Equations (1) – (3) is treated in more detail in the paper by Hari (1980).

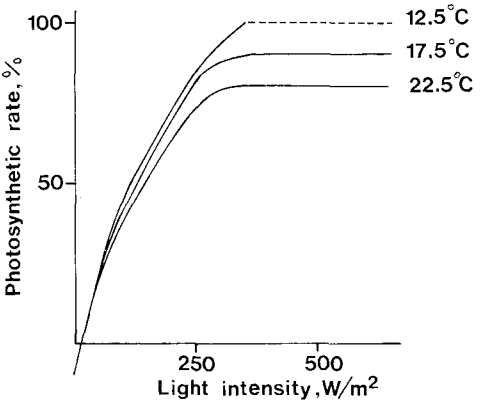


Figure 1. Dependence of photosynthetic rate on light intensity and temperature.

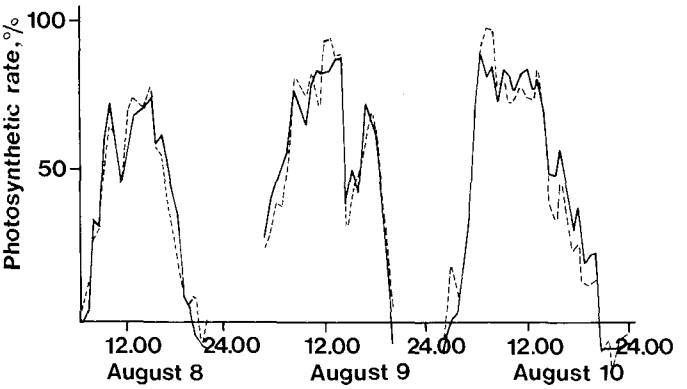
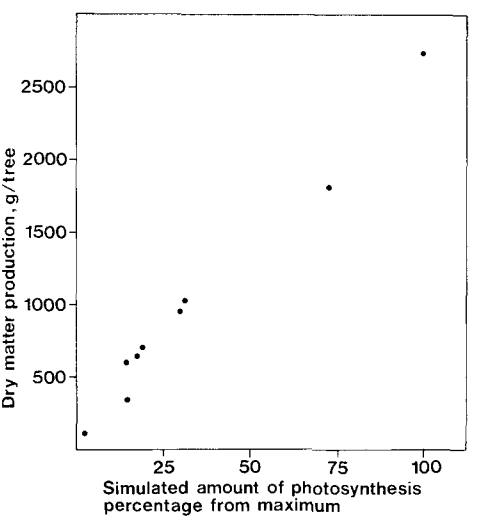


Figure 2. Measured (solid line) and predicted (dotted line) photosynthetic rates. Prediction is carried out by interpolation of the relationships in Figure 1.

Figure 3. Relationship between simulated total amount of photosynthesis and amount of dry matter production. Simulated amount of photosynthesis is the following integral:

$$P(t_1, t_2) = \int_V \int_{t_1}^{t_2} \rho\,(X)\, p(X), t)\, dt\, dV,$$

where $P(t_1t_2)$ is simulated photosynthesis during the period (t_1t_2), X space coordinates, ρ needle density, p photosynthetic rate.



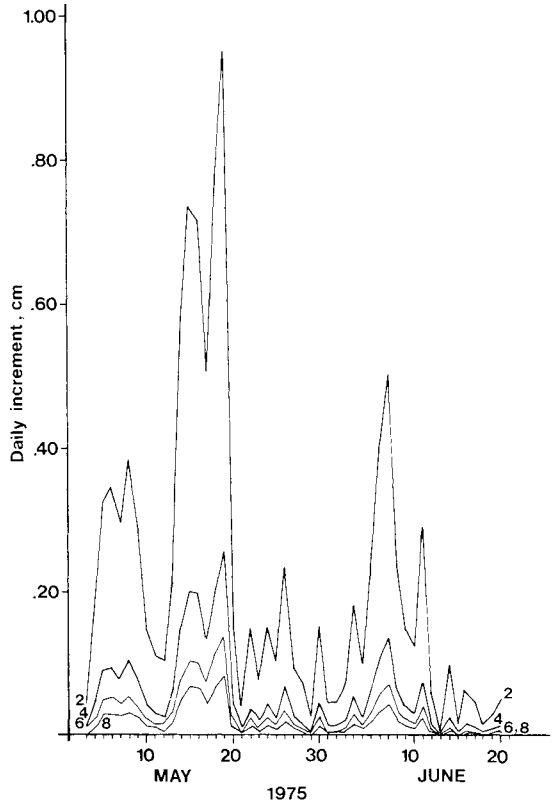


Figure 4. Daily length increments of lateral shoots of Scots pine. Numbers indicate the number of the whorl from the apex.

Adaptation of metabolic processes

The structure of a plant determines which environmental factors functions f_1 and f_2 (cf. Equations 1 and 2) depend on. Beside environmental factors, functions f_1 and f_2 include several parameters, the values of which may be of the following types: 1. species or ecotype specific, 2. specific for individuals and 3. nonconstant in the plant. A typical case where a parameter of the third type is involved is shown in Figure 4. Let α denote the set of parameters of the first type, β of the second type and γ of the third type. The differences in the functions f_1 inside a plant are caused by the spatial variation in the parameter γ

$$f_1(Y(X, t), X, S(t)) = \\ = f_1[Y(X,t), S(t), \alpha, \beta, \gamma(X)]. \quad (4)$$

There is always variation in the values of parameters α. In evolution those plants whose metabolism best fits the environment are the most capable of surviving (cf. postulate 4). Thus, in the long term, the functioning of a species or ecotype converges towards the optimum within the limits of its structure and in the location specific environmental conditions (cf. Tooming, 1970; Oster & Rokling, 1979). In addition, it is not only the values of parameters α that are changed in evolution. The whole control system of the plant changes in such a way that the values of parameters β and γ (X) become optimal within the limits of the structure of the plant and of the amounts of metabolites which are available in the actual environment of the plant or organ. Determining optimal functioning in an operational form is quite complicated. There are several criteria which can be applied, such as, 1. maximisation of the number of offspring capable of producing offspring; 2. maximisation of the life expectancy; and 3. maximisation of net photosynthesis over a prolonged period, etc. All of these are of importance for the survival of a species in a changing environment. The second and third criteria are consequences of

the first and they carry the contribution of one single process to the maximisation of the number of offspring capable of producing offspring. The values of parameters α can most probably be determined by means of the first criterion and those of β and γ (X) using the second and third criteria.

As an example, the growth processes demonstrated in Figure 4 are studied in more detail. Let b(t, X) denote the production rate of structural dry matter. It depends on the temperature and on the physiological stage of development, S_a

$$b(X, t) = L(X)\ cb(S_a(t))\ h(T(t)) \tag{5}$$

where L is the growth level which varies inside the canopy, cb is the effect of self-regulation on growth and h is the effect of temperature. This model is in quite fairly satisfactory agreement with the empirical results (cf. Hari *et al.*, 1977; Vuokko *et al.*, 1977). The growth level, L, is adjusted by the plant in such a way that new leaves produce maximal amounts of photosynthates within the limitations of the structure of the tree. Thus, we solve the following optimization problem:

$$\max_{L} \left\{ \int_{t_1}^{t_2} \int_{V} \rho_{leaf}(X)\ p\ (X, t)\ dV\ dt \right\} \tag{6}$$

The mass of new tissues (leaves, stem and roots) equals the amount of photosynthates available for growth, in practical calculations being the total amount of photosynthesis during the preceding year.

Processes at the stand level

Let vector m_{com} denote the rates of the metabolic processes of a stand. It is obtained by summing the rates of the individual trees together

$$m_{com}(t) = \Sigma_i\ m_{pl\ i}(t) = \\ = \Sigma_i \int_{V} \rho_i(X)\ m_i(X, t)\ dV \tag{7}$$

where i refers to the individual number, i. The above summation is a rather simple operation, but it allows utilization of the third postulate, since according to Equation (1) $m(X, t) = f_1(Y(X,t), X, S(t))$ Thus

$$m_{com}(t) = \\ = \Sigma_i \int_{V} \rho_i(X)\ f_1\ (Y(X, t), X, S(t))\ dV \tag{8}$$

Conclusions

All the postulates of the studied approach were, in principle, formulated and applied in developing the present model. In practice, there are, however, difficulties in deriving and in quantifying the functions needed to describe the relationships between different processes and the environment. However, the present model seems to be a promising way to introduce different kinds of environmental and phytometric data into the analysis. The formulation of the postulates required by the study approach demonstrates also that very different phenomena of plant functioning and structure can be reduced to a few principles. Such principles are needed to improve the formation of the hypothesis and the data acquisition applied for their verification.

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The Number and Quality of the Driving Variables Needed to Model Tree Growth

J. J. Landsberg[1]

Long Ashton Research Station, Long Ashton, Bristol, BS18 9AF, U. K

Abstract

Tree growth may be described by simple models with a high empirical content and response times of the order of a season, but if these are to be of general value they should be consistent with shorter period growth models written in terms of the underlying physiological processes. The driving variables for the models at all levels are weather factors: radiant energy, air temperature and humidity and wind speed. Soil water and nutrient conditions modify the responses to these factors. The accuracy with which driving variables must be specified for simulation, or measured for model testing, depends on the response time of the biological processes being simulated. For short-period (low organisational level) models detailed, accurate values of driving variables are required; as the response time of processes increases the detail and accuracy required of driving variables decreases. Variables such as leaf temperature in low-level models and soil water balance in higher level models may have to be calculated from weather data. The relationships between in-canopy conditions and standard weather measurements must be studied and, for long term models, the spatial and temporal variations in weather conditions are important.

Introduction

Before considering the question of the number and quality of driving variables required to model tree growth, we have to be clear about what we mean by models and what the objectives of the modelling exercise are.

We may define models as formal statements of hypotheses, summaries of our knowledge, at a particular level or levels, about how systems respond to stimuli. When such statements are made in mathematical terms it usually becomes clear that our knowledge is incomplete and assumptions have to be made about how parts of the system work. The consequences of these assumptions can be explored either algebraically or numerically and it must be possible to test them, and the model as a whole, experimentally. Models also serve as a framework within which the results obtained from experiments on parts of the system can be evaluated in relation to other parts of the system and to the system as a whole.

A model at any level may be considered adequate if predictions made with it are not invalidated by experimental tests, i.e. given that the input data (driving variables) are accurate the output from the model must not be significantly (statistically) different from values of the output variables measured to provide a test of the model.

It is sometimes argued that models may be divided into two groups: "management" and "explanatory" models. The main objective of management models is said to be to obtain results which provide information about the behaviour of a system, e.g. growth of trees, in response to stimuli, without much concern for the mechanisms responsible for the responses. Explanatory models are mechanistic, i.e. an attempt is made to describe the responses of the system to stimuli in terms of the effects of changing conditions on the mechanisms (physiological processes in the case of trees) which determine the behaviour of the system. I do not consider this distinction to be useful; as far as possible all models should be formulated in terms of mechan-

[1] Present address: CSIRO, Division of Forest Research, Canberra, Australia.

isms, although it is often neccessary to resort to empiricism because we do not know enough about the mechanisms underlying observed responses to incorporate them in a model. Models intended for use as management tools are likely to be more useful and reliable if they are based on, and incorporate, the mechanisms underlying observed and simulated responses.

I contend that a model of tree growth which will perform well under a wide range of conditions, and serve for evaluating the consequences of changes in physiological or environmental conditions should consist of, or at least be based on, a hierarchy of models at different organisational levels. These would range from models of particular physiological processes, with relatively short response times, to "lumped" models describing the behaviour of complex systems over longer time periods. These lumped models will be much simpler than the process models, but it should be possible to generate the relationships used to formulate them from the process models. In this paper I outline the characteristics of a set, or hierarchy, of models, which would describe, and could be used to analyse, tree growth in relation to environmental factors (see Figure 1). The environmental factors are the driving variables. The

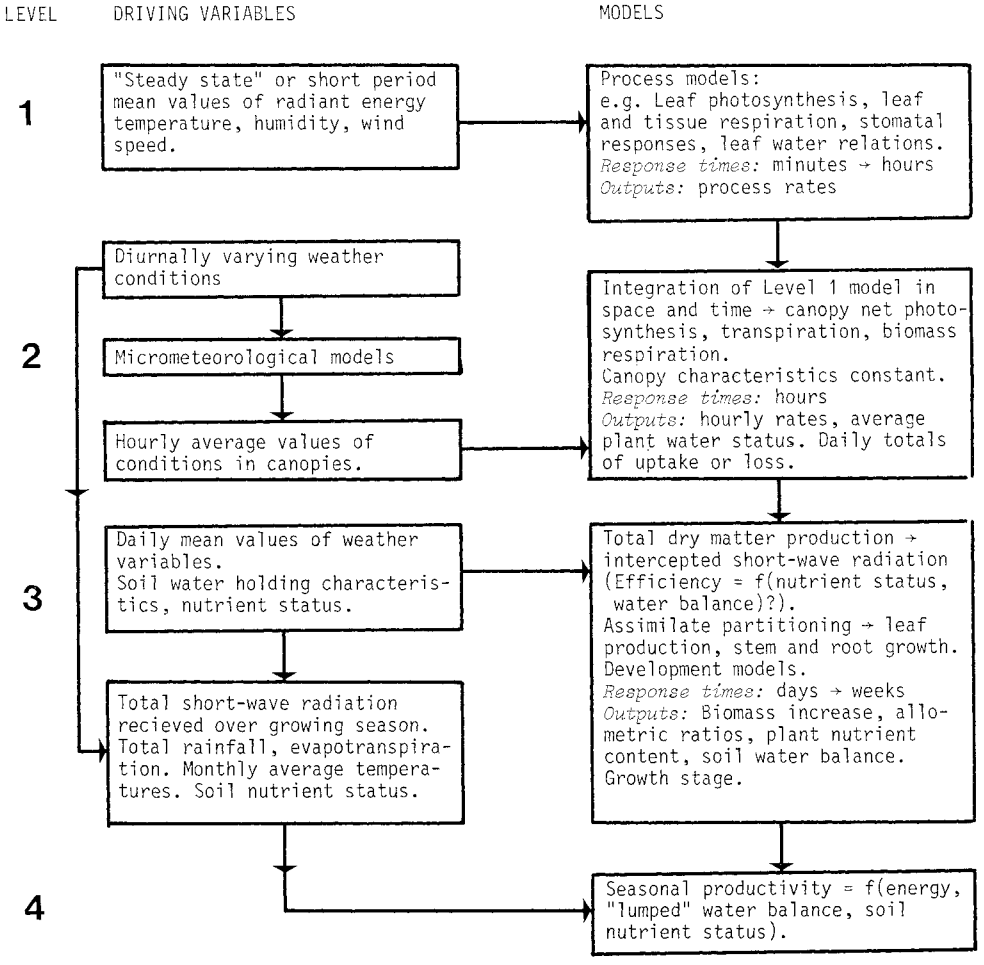

Figure 1. Outline of hierarchy of models which could provide a means of evaluating the effects of changes in driving variables on the growth of trees over periods ranging from hours to seasons.

set spans the range of biological organization levels from process models, with response times of the order of minutes (Level 1) to forest productivity models (Level 4). The accuracy and detail with which the driving variables must be specified at each level are discussed in relation to the requirements of the model(s) at that level.

A hierarchy of models

Level 1. Very short-period models (response time minutes→hours), dealing with processes at leaf level such as photosynthesis, respiration, stomatal functioning, transpiration and water relations.

At this level models may be empirical and the process may be described by relationships obtained by fitting curves to data. It may or may not be possible to attribute biological significance to the parameter of these curves; for example a commonly used equation describing leaf net photosynthesis as a function of photon flux density contains terms equated with mesophyll resistance and the quantum efficiency of CO_2 uptake. Stomatal functioning, which is currently the subject of a great deal of research effort, can be adequately described (at least for some plants) by an equation in terms of short-wave radiant energy and air humidity (see, e.g. Thorpe *et al.*, 1980). Transpiration rates are governed by the leaf energy balance and changes in leaf water potential are almost linearly dependent on changes in transpiration rate. Photosynthesis, respiration and stomatal behaviour may be affected by leaf age, condition and nutrient status; these factors may have to be considered when modelling these processes.

As far as the physics of plant environment interactions are concerned Level 1 models will deal with the properties of leaves in terms of absorption and reflection of energy and the partitioning of absorbed energy. This involves information on boundary layers and, of course, stomatal conductance.

Level 2. Short-period models (response time hours→days). Level 2 models may include processes such as net photosynthesis, transpiration rates and (driving variables) micoclimate conditions in the canopy (where "canopy" refers to the population of trees, regarded as an entity). Canopy photosynthesis depends on radiation interception and the photosynthetic characteristics of the leaves which form the canopy. We therefore require radiation interception models and equations describing the temperature, humidity and wind speed profiles which develop within canopies under specified weather conditions.

This does not imply acceptance of the idea that bulk exchange processes within canopies can be described by one-dimensional equations assuming horizontal homogeneity. There is now ample evidence (e.g. Legg & Long, 1975; Legg & Monteith, 1975) that this does not exist in canopies. Current theory is inadequate to deal with the problem. However, if average values of temperature, humidity, short-wave radiation and wind speed in layers in the canopy can be calculated these can be combined with Level 1 models. Integration over space and time leads to Level 2 outputs.

The application of Level 1 models to canopies requires reliable information on canopy structure and leaf-age distribution. These are usually arbitrarily specified but should come from models of dry matter distribution.

Level 2 models can provide estimates of tree growth (carbon balance) and the water balance of canopies on an hourly and daily basis, reflecting the effects of changing driving variables through factors such as leaf water status and stomatal conductance. They are likely to be much too detailed, and use too much computer time, to be run over periods longer than a few days, but can be used to assess the accuracy of Level 3 models – and perhaps to generate them (see below).

Level 3. Longer period, simplified simulation models (response time days→weeks).

Level 3 models may be based on empirical relationships between the carbon balance of canopies and, say, total daily short-wave energy income. (The best relationships are likely to be obtained from absorbed short-wave energy. In dense canopies it can be

assumed that all the incident energy, except that reflected, is absorbed by leaves.) In agricultural crops the parameters of Level 3 models can be derived from a series of destructive harvests to determine weight changes at short intervals through one or more seasons, but in the case of trees it may be necessary to derive Level 3 models from Level 2 models, run for a number of days and a variety of conditions.

At Level 3 we become concerned with nutrient uptake and with the allocation of assimilate to different parts of the tree, i.e. with shoot growth, stem diameter increase and root production. Since knowledge of the mechanisms of nutrient uptake, and those controlling assimilate partitioning is currently inadequate for mechanistic modelling, both these are likely to be dealt with empirically. Factors such as the effects of water deficits on growth (which involves both assimilate production and partitioning) would be dealt with at Level 3, where water deficits are likely to be modelled in terms of daily or weekly soil water balance, with some form of stress index being used to characterise the effects of the deficits. Calculations of the water balance would require information on rooting depths, soil water holding characteristics, rainfall, rainfall interception and the evaporation of free water from canopies, and transpiration rates. Models at this level may also include the effects of temperature on growth rates and should certainly include developmental processes. Bud development, the time to bud break and shoot growth can be treated as functions of temperature. It is essential to develop models of leaf growth and senescence for use in Level 2 models because if arbitrary descriptions of canopy structure are used then no matter how good the physics and physiology at Level 2 the results at Level 3 may be almost meaningless. This is a case where there must be feed-back from a Level 3 model to Level 2 models.

Level 4. Long period models (response time, seasons).

Level 4 models are likely to be mathematically simple, perhaps incorporating relationships between total wood production and amount of short-wave radiant energy received during a growing season. The parameters of this relationship may be modified by some form of "lumped" water balance and possibly a term for the nutritional status of the soil. The data underlying Level 4 models may be annual harvest data from many sites (preferably where trees have been subdivided into their component parts), studies on litter turnover and characterisation of soil conditions. It should also be possible to generate a Level 4 model from a Level 3 model.

Driving variables and test measurements

Driving variables and test measurements are considered together because in deriving the parameter values for models, and in testing the models, the driving variables have to be accurately measured.

The driving variables for Level 1 models are short-wave radiant energy, air temperatures, humidity and wind speed. The parameters for empirical models of processes such as leaf photosynthesis and stomatal behaviour are often obtained from gas-exchange measurements made under steady-state conditions in controlled-environment cuvettes. They may also be derived and tested in the field using cuvettes which track ambient conditions or in which the level of individual factors can be controlled. Whether gas exchange measurements are for parameter establishment or model testing purposes, measurements of the environmental factors should be made by instruments which respond faster than the physiological processes under study. Where the work is being done under varying conditions integration should be used to obtain mean values over periods which may vary from a few minutes to half an hour, depending on the response time of the biological processes.

In many cases the value of the driving variable will be a function of the measured variable, e.g. leaf photosynthesis rates depend on absorbed radiant energy, not on incident energy (although the two may be linearly related); leaf energy balance and the partitioning of absorbed energy – leading to estimates of transpiration rates – depend on leaf-air

temperature differences, so we must calculate leaf temperatures; tissue respiration rates depend on tissue temperature. Good models of the physical relationships between plant organs and environmental factors are essential pre-requisites for Level 1 modelling.

The driving variables for Level 2 models are short-wave radiant energy, air temperature and humidity and wind speed in canopies, and canopy net radiation. To run Level 2 biological models the appropriate values of these driving variables may be calculated from measurements made above the canopy or even at nearby meteorological sites. Cowan (1968) and Waggoner (1975) have developed models with which conditions inside canopies can be calculated from boundary conditions which must be specified for the top and bottom of the canopy (see also Gourdriaan, 1977). Radiation interception models may be highly complex (e.g. Norman & Jarvis, 1975) or relatively simple (Halldin *et al.*, 1979). Given an estimate of mean wind speed at any point within a canopy, boundary layer resistances to the exchange of water vapour and CO_2 can be calculated. The models for this may be quite complex, including factors such as the effects of mutual aerodynamic interference between leaves or clumps of leaves (Landsberg & Thom, 1971; Landsberg & Powell, 1973).

Level 2 simulations would normally be based on hourly mean values of the driving variables, whereas in reality factors such as radiation are highly variable over much shorter periods. Radiation measurements, made both above and within canopies to establish or test the necessary microclimatic models should, therefore, be integrated. Temperature measurements should be made with accurate but relatively slow-response sensors and wind speeds measured with anemometers which totalize wind run over the selected time interval.

Photosynthesis, respiration and transpiration rates calculated by Level 2 models may be tested using cuvettes, or by estimating fluxes above the canopy from profile measurements. Leaf water potentials have to be tested by measurements made at intervals to sample a range of different conditions. In principle it is possible to calculate transpiration rates for different layers in canopies, and hence leaf water potentials at different levels, but these calculations involve considerable uncertainties and interpretation of the results is dubious. A more promising approach has been adopted by Edwards (1980). He used a model of water movement through the stems of trees, which includes storage (capacitance) and the changes in hydraulic conductivity with stem water content, to simulate changes in water potential with time at different heights in the stem The model assumed all transpiration to be from the top of the stem. The development and testing of such models is important but must be accompanied by evaluation of the effects of different periods of water stress (low water potential) on growth processes.

The inputs to Level 3 models will be daily values of radiation, average daily temperature, total daily water use and rainfall. Since Level 3 models involve water balance calculations and growth estimates, testing them necessarily involves measurements of soil water balance, growth measurements (shoot length, trunk diameter measurements) and observations on processes such as bud development and leaf age classes. Extensive root sampling would provide valuable data, contributing information on assimilate partitioning. Measurements of factors such as litter fall would also be used to test Level 3 models.

The accuracy required of data used for Level 3 simulations is lower than that for Level 2. For example temperature sensors used to make measurements to test Level 2 models should be accurate to about $\pm 0.1°C$, whereas for Level 3 work there is no need for accuracy better than about $\pm 0.5°C$. Similarly anemometers used to measure wind speeds for Level 2 models would need to start at about 0.2 m s^{-1} and to have virtually no overrun. Accurate wind speed measurements are not required for Level 3 models and anemometers need only provide wind run data, over periods of not less than an hour, to about $\pm 10\%$. Radiation data to test Level 2 models must be derived from measurement. For Level 3 it may be adequate to use estimates

of radiation derived from sunshine hours, providing that the time interval is of the order of a week. Such estimates are certainly adequate for Level 4 simulations.

It will be clear from the above that the inputs to Level 4 models can be obtained from national meteorological networks and are not likely to be accurate when applied to any particular site. This is not important since uncertainties arising from factors such as the seasonal pattern of temperature (latest frost in spring, rate of temperature rise) and rainfall distribution may well have much greater effects on final yield than the lumped driving variable values used in the model. For this reason Level 4 models are likely to be very insensitive to short-period changes in weather and are mainly of value for long term estimates of growth and production.

Concluding remarks

In this paper I have developed the idea that models, which should be regarded as formal expressions of hypotheses, or descriptions of how we *think* systems work, may be written at any number of levels, from cellular to ecosystem.

Obviously the processes and driving variables suggested here as suitable for inclusion in the models at various levels are only a sample. It will be apparent that there is a considerable degree of overlap between models at different levels. This is inevitable and necessary, although the response times on which these levels are based are arbitrary and themselves overlap. It should also be clear that there is no dichotomy between mechanistic or explanatory models and (so-called) management models. All models contain elements of empiricism – relationships derived from observations or measurements without any reference to the underlying mechanisms. We can always argue that a model is empirical, and that it could be written at a lower level. The process of photosynthesis provides a good example. There is a great deal of research on photosynthesis at the level of processes such as electron transfer and enzyme kinetics. From this we may work up through several levels to what I have called a Level 1 model – the uptake of CO_2 by leaves, described in relation to their light regime. The *objective* in building a model may dictate, to a large extent, the amount of empiricism which the model-builder is prepared to tolerate.

Although I have proposed earlier that higher-level models may be synthesised from lower-level, more mechanistic, models, it is not *necessary* to work in this direction. It may often be convenient, and a more profitable way of working, to obtain an empirical higher-level model early in a programme, and proceed from there "downwards" to examine the mechanisms which contribute to, and explain, the responses described empirically. As the lower-level experimentation leads to the development of reliable models at that level the higher level models may be modified and improved. This 'up and down feed-back' can be applied across any number of organisation levels.

It is evident that the number and quality of the driving variables needed for modelling is not the same from one level to the next. The number increases from Level 1, where only one or two driving variables may be needed for each model, to Level 2, where many are required to simulate, in detail, processes in canopies. At both these levels considerable precision is required in specifying driving variables, and considerable accuracy is required in their measurement. The requirement for both are less stringent at Level 3 and not critical at Level 4.

The remarks made earlier about canopy structure deserve further emphasis here. It is essential that progress be made in modelling the development of canopy structure in terms of leaf area and its spatial distribution, and leaf age classes. Canopy structure should *not* be treated as an input – it affects every aspect of Level 2 and Level 3 models and no amount of accuracy in other measurements will compensate for erroneous specification of the canopy structure. The errors which will result can be assessed by sensitivity testing.

If the end point of a research programme is, say, an accurate Level 3 model, it is worth including in that programme analysis of the relationships between conditions inside tree canopies and the weather data obtainable

from standard, national network, meteorological observations. The network observations are the only long-term source of data available, and if models are to be used for the evaluation of yield potential at different sites, growth in different seasons and assessment of the effects of management practices, e.g. thinning, irrigation, fertilization, then these are the data which will have to be used as inputs. The spatial and temporal variation in weather factors (frequency of occurrence of extreme events, variation about means etc.) should also be investigated.

I said in the Introduction that models should be testable, and mention has been made of the type of measurement needed to test models at the different levels. No attempt has been made here to discuss the techniques involved, which is outside the scope of this paper. Although it should not be necessary, it is perhaps worth pointing out that measurements made to test models should be entirely independent of those used to derive the constants and coefficients of the equations. Test procedure essentially involves simulating tree responses from (measured) inputs, and comparing these with measured responses. It follows that the measurements must be appropriate to the level of the simulation. Because it is often technically possible to make better physical than biological measurements it is sometimes tempting to measure driving variables more accurately and/or record them more frequently than is justified by the biological measurements which can be made to test the model. This may lead to spurious precision in the output, which cannot be tested; it is a waste of time and effort and can be avoided by proper sensitivity testing to evaluate the quality *necessary* for driving variables. Sensitivity testing is also an essential tool when moving from a lower to a higher level – to what extent can variables be "lumped", or averaged, without unacceptable loss of sensitivity in the outputs?

In summary, modelling is a tool for making quantitative predictions about the behaviour of a system in respect to varying inputs. Models may be written to describe parts of the system, or processes within it, or to describe the behaviour of the whole system. Models become mathematically simpler as the scale of the system increases, and accuracy in specifying driving variables becomes less critical.

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Plant Water Relations in Models of Tree Growth

P. G. Jarvis

Department of Forestry and Natural Resources, University of Edinburgh, EH9 3JU, U.K.

Abstract

The assemblage of submodels considered necessary for a stand growth model is presented. This assemblage contains several submodels which in themselves form a stand water–use model but have an important influence on the growth model either because their outputs are needed as inputs to some of the growth submodels, or because of feedback between the growth and water relations submodels. For example, output from the soil and plant water relations submodels is required as input to the submodels concerned with leaf phenology, stomatal conductance, photosynthesis, nutrient status and fine root growth.

A tree water relations model is presented. This model predicts water flow, water content and water potential at points in the tree between the soil and the atmosphere, both where these variables can be measured in the tree with current techniques, and where they cannot because the techniques are inadequate. The model takes storage into account and predicts realistic reductions in the diurnal amplitude of these variables, as well as phase shifts, in the tree at ground level, as compared with the values in the canopy.

Introduction

Models of water use by vegetation and of plant water relations have proliferated rapidly over the last few years (see the review by Jarvis *et al.*, 1981). There are two main reasons for this. Firstly, water is an important and often scarce resource, even in temperate regions, so that considerable interest attaches to attempts accurately to predict the loss of water from vegetation by both evaporation and transpiration. Such predictions are important in a hydrological context and can assist in making decisions with regard to land use. For example, a key question at the present time is whether trees should be planted in watersheds when the yield of water is the product of major importance. Water-use models, therefore, can themselves have a significant influence on the plant growth on an area of land by influencing the use of the land and its vegetation cover. For example, simple models of water use and soil and plant water relations in a climate with a seasonal, winter rainfall can lead to an assessment of the suitability of different crops for the area (e.g. Morgan, 1976). Water use itself is also very relevant to production, especially if supplementation of natural precipitation incurs a cost, because the amount of production per unit of water used may be a more useful crop and site parameter than growth alone.

Secondly, evaporation and transpiration are the driving variables for the flow of liquid water in the soil-plant-atmosphere catena so that their rates affect the water content, water potential, solute potential and pressure potential throughout the catena.

Some or all of these state variables are likely to influence growth and growth processes when their values become extreme (see reviews by Hsiao, 1973; Slatyer 1969, 1973; Boyer & McPherson, 1975; Begg & Turner, 1976; Fischer & Turner, 1978; Lawlor, 1979). In view of the regular appearance every two to three years of authoritative reviews of the influence of water stress, and particular components of stress, on growth processes, it seems unnecessary to attempt to review the evidence here. There is no doubt that the flux and state of water in the soil and plant has a substantial influence on growth. Instead I will indicate how I think water relations parameters might be adequately included in a growth model.

Stand growth models – time to begin

Models of stand growth and water relations which are mechanistic and largely deterministic provide a means of explaining and understanding variations in yield from site to site and year to year. A very good assessment of what can be achieved is to be found in the recent review by Loomis, Rabbinge and Ng (1979) entitled "Explanatory Models in Crop Physiology". Useful recent models aimed at the explanation of community level crop behaviour have been developed for corn (de Wit *et al.*, 1978), rice (Iwaki, 1975), wheat (Morgan, 1976), soybean (Curry *et al.*, 1975), sugarbeet (Fick *et al.*, 1975), cotton (Duncan, 1972), alfalfa (Holt *et al.*, 1975), and potatoes (Ng & Loomis, 1981). These models have had important impact on, for example, the breeding of cereals in Mexico and the Phillipines and on the management of crops of improved varieties (see Evans, 1975 and Milthorpe & Moorby, 1979). It seems highly likely that similar useful results will also be achieved from models of forest crops in the future.

In addition a model of this kind provides a strong framework for research. It provides a synthesis of knowledge, defines areas of ignorance and at any moment represents a highly organised summation of our understanding of the functioning of the particular processes and overall system. That is to say the model represents the best hypothesis we have about the functioning of the system.

It can always be argued that the concepts and the data we have may prove not to be adequate to define either the physiological processes or the environmental variables. However, I think the concepts and the data we now have are sufficient to make it worthwhile making a start on forest stands and I think it is timely to begin now. A model may not do all we want and accuracy may be poor in some parts. At the very least, however, we will learn where to concentrate research effort in order to make the biggest improvements. It will always be possible to argue that we don't have an adequate basis to begin, but unless we do make a start we shall never know how far we have come or how far to go to achieve a useful level of understanding.

A stand growth model

A mechanistic model of the growth of a stand of trees needs to consist of a number of partially discrete submodels each of which can be developed or totally replaced as new ideas and new data become available. Table 1 lists

Table 1. The 14 submodels proposed are the following:

1. *Leaf phenology and growth:* 1 *O/P – number of leaves of particular age and size at any time, leaf area index, leaf area density. **INT-week.
2. *Radiation interception:* O/P flux densities of visible and net radiation on sunlit and shaded leaves. INT – hour.
3. *Stomatal and canopy conductance:* O/P – stomatal conductance of leaves of different ages and position; canopy conductance. INT – hour.
4. *Leaf and canopy photosynthesis:* O/P – CO_2 fixed by leaves of different ages and position; canopy photosynthesis. INT – calculated hourly, summed over each day.
5. *Transpiration:* O/P – amount of water transpired by leaves of different ages and positions; total transpiration from the canopy for unit ground area. INT – calculated hourly, summed over each day.
6. *Carbon allocation:* O/P – amount of carbohydrate allocated to leaves, stems, fine and coarse roots. INT – day.
7. *Respiration:* O/P – amount of CO_2 lost in growth and maintenance in leaves, stems, fine and coarse roots. INT – day.
8. *Evaporation:* O/P – amount of water evaporated from the wet canopy, branches, stem and ground. INT – calculated hourly, summed over each day.
9. *Plant and soil water status:* O/P – flow, amount and potential of water in leaves, stem, roots and soil layers. INT – hour.
10. *Plant and soil nutrient (nitrogen) status:* O/P – nutrient concentrations in solution in soil layers and in the plant. INT – day.
11. *Branch and stem growth:* O/P – amount of branches; volume and weight of early and late wood. INT – week.
12. *Fine root growth:* O/P – birth and death of fine roots; amount at any time. INT – week.
13. *Coarse root growth:* O/P – amount and extent of coarse roots. INT – week.
14. *Population development:* O/P – number of trees of particular size and sound status at any time. INT – year.

* O/P = output

** INT = time interval at end of which the output is accepted for use.

the submodels that I envisage forming the backbone of a practical and useful stand growth model. In addition a submodel is required for the *weather inputs* which are completely independent of the interactions between the submodels.

The first five submodels are more than adequate in their degree of mechanistic details and have been reasonably well thought out at the present time. They have been developed for the closed canopy situation and have been run individually for periods of days. The output from each of these five submodels is currently being tested against measurements made over short periods at different times of the year in stands of Sitka spruce and Scots pine in forests at Fetteresso, Thetford, Roseisle and Rivox. For example, the output from submodels (2) and (3) is being tested against measurements of canopy conductance and CO_2 influx made both with porometers and $^{14}CO_2$ methods and with micrometerological (Bowen ratio) methods. The five submodels have been merged into a preliminary canopy process model which has been run for a closed Sitka spruce canopy over a 12 month period. We are now in the process of developing the additional submodels.

Without doubt some of the other submodels will initially be extremely empirical with considerably oversimplified functions relating output to input. For example, in the particular case of assimilate partitioning and allocation to different growing areas, we do not know a great deal about conifers. However, we know more now than a few years ago as a result of the recent work of Ericsson (1978, 1979) and Ericsson *et al.* (1980) on Scots pine and Chung & Barnes (1977, 1980) on loblolly pine. In particular recent interest in pests and diseases has sparked off a lot of new work on carbon allocation, and although much of this work is not on coniferous trees, it does allow the development of a conceptual framework (e.g. McLaughlin & Shriner, 1980). Whilst the use of several submodels which are essentially black boxes introduces an undesirable element of empiricism at several points, the precise definition of the areas of least knowledge with respect to stand growth processes is in itself valuable and provides useful guidelines for the investment of research effort in the future.

We also have developed a submodel (9) on lodgepole pine at the Forest of Ae (see Jarvis *et al.*, 1981). The above ground part works well but further work on the root and soil end is needed. This submodel is described in more detail later. We have not as yet done any work on the other eight submodels although we have clear ideas as to how we would proceed.

The inputs to the submodels are driving variables such as solar radiation, windspeed, air temperature and dewpoint temperature. Soil physical characteristics such as rooting depth, bulk density and water retention properties are also required together with starting values for nutrient and water status. The outputs from the submodels are the rates and integrals of derived variables such as carbon fixation, transpiration and evaporation, nutrient and water uptake and internal contents, assimilate allocation, rate of respiration and growth of leaves, shoots, stem and roots. Clearly some of these submodels require as input the output of others. For example, leaf area is required for radiation interception, stomatal conductance is required for carbon allocation and so on. These interrelationships are shown in the interaction matrix in Table 2.

Values for as many of the parameters as possible have been obtained from our own field work and laboratory experimentation using a range of techniques. For example, the values of the parameters in the relationship between stomatal conductance and light, temperature and vapour pressure deficit vary seasonally. These values have been found using a non-linear least squares package and field data obtained in the spring, early summer, late summer and autumn. An optimisation procedure has similarly been used to find values for the mesophyll conductance parameter at different times of the year. Values for other parameters will be derived from published experimental work as far as possible. Each submodel will then be analysed for sensitivity to the driving and state variables and the values of the parameters and will be

Table 2. Interaction matrix showing how the output from some submodels is input for others, e.g. the output from the conductance model (3) is used as input for the photosynthesis (4) and transpiration (5) models.

Submodel giving output	Submodel receiving input													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. Phenology	○	×				×								×
2. Light/Radiation		○	×	×	×			×						
3. Conductance			○	×	×									
4. Photosynthesis				○		×								
5. Transpiration					○				×					
6. Allocation	×					○	×				×	×	×	
7. Respiration							○							
8. Evaporation								○	×					
9. Soil & plant water	×			×					○	×		×		
10. Soil & plant nutrients	×		×							○				
11. Stem/branch growth		×			×						○			×
12. Fine root growth					×							○		
13. Coarse root growth					×								○	
14. Population			×											○
15. Weather variables	×	×	×	×	×	×	×	×	×	×	×	×	×	

tested, as far as possible, against independent measurements.

The submodels necessarily vary in their level of resolution depending on the state of knowledge and quality of information available about the processes. The basic unit of time resolution is one day and the output of the submodels will be expressed in daily totals as far as possible. These will be integrated through running the model into weekly and annual growth rates. For some of the submodels for which considerable detailed information is available (e.g. carbon assimilation, transpiration), the initial time period for calculation is one hour and daily totals are obtained by accumulation of hourly values. In other submodels, lacking the same degree of detailed information, daily totals will be computed directly and in one or two cases, if the basic information is lacking, longer initial time periods may be forced upon us. Nonetheless, all the submodels will be required to be consistent with one another so that submodels with an initial short time period resolution can be combined with submodels which of necessity integrate over longer periods.

This assembly of submodels should be sufficient to produce a model of stand growth and tree population from planting through to harvest with an acceptable degree of simplification. The model will accommodate the distribution of growth between individual trees when complete. Submodel (14) will attempt to simulate the emergence of dominants, subdominants and suppressed trees so that the distribution of volume increment in the stand should be predictable. However I would note in passing that this point is only relevant if managers come off the fence and define the specific objective for which particular stands are being grown, e.g. for saw logs or for pulp. Later we hope to be able to examine the effects of management operations on the stand with the use of the model and to determine the likely results of particular 'treatments' such as planting density, thinning regime, fertilizer applications and eventually also the impact of diseases and pests. Before we can get to this stage, however, we must have a good qualitative and mechanistic model of the growth and development of the stand.

It is important that the submodels should be individually testable and tested over a wide range of conditions and that the end result of the model should also be tested. Since the same harvestable yield can be

achieved in different ways, we must be able to calculate with acceptable accuracy, not only the final yield, but also the state of the stand at all stages of growth. This will demonstrate that the responses of the processes to the environmental variables are being modelled at least approximately correctly.

The model will then be tested against growth data from field plots and field experiments, which have been regularly measured. The model is deterministic and predictions will be made of canopy processes and stand growth for different sites with different input variables, including weather and climate and site characteristics such as soil physical properties and nutrient status. From a number of such comparisons, it should be possible to identify and improve those parts of the model which are least accurate or realistic and arrive at an acceptable degree of simplification and validation. It must be emphasised most strongly that these are *not* curve fitting exercises. A model is a very inappropriate tool for curve fitting. It would be easy enough to force the model to fit stand data by optimisation but this would defeat the whole purpose which is to enhance our understanding of how the system functions thereby enabling predictions to be made over a wide range of conditions.

The role of the water relations submodel in the model

The interaction matrix in Table 2 indicates that output from the plant and soil water status submodel is required as input to the submodels concerned with leaf phenology and growth, stomatal conductance, photosynthesis, plant and soil nutrient status and fine root growth. A case could be made for introducing plant water status into some of the other submodels, e.g. carbon allocation (Fischer, 1980), but, in the first instance, sufficient complexity will be introduced by dealing with the main effects. These are summarised in a little more detail below.

(1) Leaf phenology and growth. The formation of leaf primordia, leaf elongation and leaf retention can all be considered as functions of xylem water potential in the twigs at appropriate times (e.g. Stransky & Wilson, 1964; Clements, 1970).

(3) Stomatal and canopy conductance. Stomatal conductance can be considered as functions of both current leaf water potential, or bulk turgor pressure, and the previous water stress history (e.g. Beadle *et al.* 1978, 1979; Turner, 1979, Turner & Jones, 1980). In several conifers, stomatal conductance also responds sensitively to changes in the humidity of the ambient air probably as a result of local reductions of turgor pressure in the guard cell complex. These may be caused by transpiration from the guard cell complex outside the stomatal pore, coupled with a significant liquid flow resistance between xylem and epidermis (Jarvis, 1980).

(4) Leaf and canopy photosynthesis. Effects of water stress on the photochemical, electron transport and carbon cycling partial processes can be treated by considering the mesophyll conductance as a function of plant water potential (e.g. Beadle *et al.*,1981).

(10) Plant and soil nutrient status. The mineralization, concentration and movement of nutrients in the soil solution can be regarded as a function of soil water content (Nye & Tinker, 1977) and movement in the plant can be considered as a function of the liquid flow rate (e.g. Greenwood *et al.*, 1974).

(12) Fine root growth. The growth and death of fine roots is very sensitive to small changes in water content and potential in the upper soil horizons (e.g. Ford & Deans, 1977).

Making use of Table 2 in the vertical dimension shows that the main inputs to the plant and soil water status model are weather variables and the output from the submodels concerned with transpiration and evaporation. These are considered in a little more detail below.

(5) Transpiration. The transpiration rate from the canopy can be calculated using the Penman-Monteith equation as a function of weather variables and stomatal and boundary layer properties (e.g. Monteith, 1965; Jarvis & Stewart, 1979; Jarvis, 1981).

(6) Evaporation. The evaporation of intercepted water from the canopy can be calcu-

lated using the Penman-Monteith equation for evaporation (e.g. Jarvis & Stewart, 1979) coupled with a running water balance of the canopy (e.g. Rutter *et al.*, 1975; Rutter & Morton, 1977).

Thus making use of the output from the transpiration and evaporation submodels, the plants and soil water status submodel should provide estimates of the amounts, potentials and flows of water at any point in the trees and the soil.

A tree water relations model

A model of water flow from soil to atmosphere through the root, stems and branches of individual trees in a stand has been developed in cooperation with W. R. N. Edwards, H. Talbot and J. J. Landsberg (Jarvis *et al.*, 1981). This model has all the essential requirements of submodel (9) above ground but at present requires the addition of a more realistic below ground section (e.g. that of Landsberg & Fowkes, 1978) to simulate the stratified removal of water from the soil by the roots.

In *structure* submodel (9) consists of four series linked compartments: roots, stem, branches and twigs and leaves forming a catena between the soil and the atmosphere. The stem is considered as a large number of thin slices. Outflow from the foliage is given by submodel (5). It is assumed that a particular tree will transpire in proportion to its contribution to the stand as measured by the cross-sectional area of its sapwood in relation to the total sapwood area of the stand. Canopy conductance is obtained from submodel (3) using appropriate parameters or from measurements.

Flow through the roots, stem and branches is defined by the Darcy equation, the permeability of each slice of the stem being a function if its water content. The resistance of the stem to water flow is obtained by summing the resistances of all the slices. The root, branch and foliage resistances at saturation are assumed to be fixed proportions of the total stem resistance at saturation. Both branch and root resistance are also function of water content and consequently they change in proportion to the stem resistance as their water contents change.

As a result of the reduction in xylem pressure potential consequent on transpiration, water is withdrawn from adjacent living tissues and from some of the xylem tracheids themselves. The measured capacitances of root, stem and branch sapwood indicate substantial withdrawal of water from the larger tracheids for small reductions in water potential. Currently storage in the living stem and branch tissues is ignored as being insignificant in relation to the main reserve of water in the stem sapwood (Jarvis, 1975; Whitehead & Jarvis, 1981). The capacitance of the foliage is given by a typical moisture release curve for pine needles (e.g. Jarvis & Jarvis, 1963). The *inputs* comprise instantaneous values of the following environmental, driving variables: solar or net radiation, air temperature, vapour pressure deficit or wet bulb depression and windspeed for use in submodel (5) to give the transpiration rate from the canopy. The same environmental variables, especially radiation and vapour pressure deficit are used in submodel (3) to derive mean hourly values of canopy conductance. Initial values of the following are also needed: saturated permeability of sapwood in the branches, stem and roots (treated as a function of water content), saturated water capacitance of foliage, branches, stem and roots (also functions of water content), volume of water in saturated foliage, branches, stems and roots, soil matric potential (treated as a function of soil water content) and volume of water in the soil horizons. Parameters are required for the relationships in submodels (3) and (5) and for the functions mentioned above. In addition values are needed for the following properties of the trees and stand: number of stems per hectare, length of stems, cross-sectional area of sapwood, leaf area index, length and surface area of roots.

In *operation* the water contents and potentials of the foliage, branches, stem and roots are initialised to values appropriate to saturation, after allowing for the effect of gravity, and the average matric potential in the rooting zone is specified. In response to evapo-

rative demand, transpiration removes water from the foliage. As a result the water content, water potential and permeability of the foliage are reduced. The consequent potential difference between the foliage and the branches causes an inflow of water to the foliage resulting in a new water content and potential. This sequence is repeated for the branches, the new outflow rate being equal to the previously calculated inflow rate to the foliage. For a particular time step this procedure is repeated from the branches to the top slice of the stem and from the top to the bottom of the stem, slice by slice, and then to roots, so that the water status of the entire tree is changed. Time is then incremented.

The *outputs* from the submodel are the flows of water, the water contents and water potentials at a number of points in the soil and in the tree. An example of these outputs is shown in Figure 1. Because of the water storage capacity and the capacitance of the tissues in and adjacent to the pathway, the flow of water in the stem lags substantially behind that in the leaves and branches. Indeed, flow from the root into the base of the stem rises steadily each day and shows little response to the diurnal variation in transpiration rate.

Diurnal changes in relative water content of the stem are considerable at the top but much smaller at the base so that it is not surprising that considerable difficulty is experienced in measuring them there (Waring & Running, 1978; Waring *et al.*, 1979) Diurnal changes in water potential are small in the stem and indicate that the largest flow resistance is in the branches, as was found in Sitka spruce by Hellkvist *et al.* (1974).

This model is at present a very incomplete model of the soil-plant-atmosphere catena. However, it has proved extremely useful in crystallising ideas regarding the role of permeability and capacitance in the trunk in tree water relations and it provides estimates of the tree water status variables required as inputs for the stomatal conductance, leaf photosynthesis, nutrient uptake and fine root growth submodels.

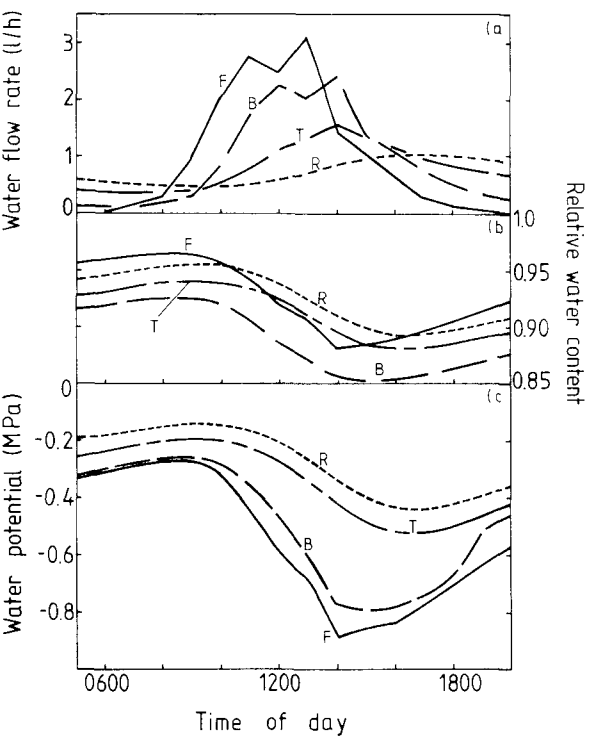

Figure 1. Simulated diurnal curves of (a) water flow rate (b) tissue relative water content and (c) tissue water potential at four locations in a tree of lodgepole pine (*Pinus contorta*) at the Forest of Ae on 8 August 1979. The curves indicate the rate of flow out of the compartment indicated by the letter or the average relative water content and water potential in the compartment:

F – foliage, B – branch, T – top of stem just below lowest branches, and R – base of stem just above the ground.

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Nutrient Flux Density Model of Mineral Nutrition in Conifer Ecosystems

T. Ingestad, A. Aronsson and G. I. Ågren

Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden

Abstract

A simple model is formulated in which the driving variable for nutrition and growth of forest ecosystems is the nutrient flux density (amount of nutrients available per unit of time and unit of area). The flux is divided in two parts, one delivered by mineralization and the other by fertilization. The model can therefore be used to analyze the dynamic effects of both nutrient sources as well as the feed-back of fertilization on the natural nutrient flux density and thus on the fertility level of the ecosystem.

The model is tested by means of data from a Scots pine ecosystem with quite reasonable results even though the analysis indicates several parameters which are difficult to evaluate satisfactorily with present knowledge. Simulation of the dynamic development of the nutrient flux density under different fertilization regimes indicates large differences in the time required to reach saturation (optimum nutrition) and maximum production. It should therefore be of the utmost interest to study further the conditions for efficient fertilization, minimum losses of fertilizers, and the long-term development of increased nutrient flux densities.

Introduction

The mineral nutrition of some plant species was studied in nutrient solutions in a series of laboratory experiments. The nutrients were supplied as different relative addition rates instead of as a variation of the generally accepted treatment variable, nutrient concentration in the solution (Ingestad, 1979a, 1980, 1981; Ingestad & Lund, 1979; Ericsson, 1981ab). An almost complete control of nutrition and growth was exerted by the relative addition rate, whether of nitrogen alone or of all nutrients in fixed proportions. In contrast, no clear relationships were found between, on one hand, external concentration and, on the other, nutrient addition rate, nutrient status of the plants, nutrient uptake rate, or relative growth rate within the sub-optimum range up to and including optimum. A clear influence of external concentration was found only at supra-optimum nutrition when a higher influx than outflux of nutrients at the root surface created increased internal concentrations.

These findings, together with an increasing amount of data in the literature (see Clarkson & Hanson, 1980), lead inevitably to the conclusion that the bulk of information on mineral nutrition of plants deals with supra-optimum problems or emanates from inadequate experiments (cf. Ingestad, 1981). Thus, sub-optimum nutrition, which is the problem of interest in natural vegetation and plant husbandry, has apparently not been produced because of the varied concentration as such but because the concentration supplied was not maintained. To maintain the concentrations and, thus, to reveal their real effects, the nutrients should have been added in agreement with consumption, i.e. as a relative addition rate. However, the studies cited above show quite clearly that plants can grow at very low external concentrations and with stable internal nutrient states and stable relative growth rates.

The relative addition rate may be regarded as a nutrient flow which quantitatively enters the plants. Negligible nutrient amounts were left in the solutions (Ericsson, 1981b; Ingestad, 1981). It was suggested by Paul Jarvis during the discussion of this paper that the term "nutrient flux density" can be used to express this nutrient flow, amount of nut-

rients available per unit of time and unit of ground area, in similarity with energy flow.

It is the aim of this paper to formulate a simple model, based upon the concept of nutrient flux density, and to demonstrate its potency to predict the development of coniferous forest ecosystems. Special interest is paid to fertilizer effects when fertilization is carried out to increase the natural flux density and therefore in amounts of the same order as are mineralized. The model is tested on a Scots pine ecosystem with data from the SWECON Project (Ågren *et al.*, 1980; Berg & Staaf, 1980; Persson, 1975, 1978), especially from the irrigation and fertilization experiment (Aronsson *et al.*, 1977; Aronsson & Elowson, 1980), and simulations are carried out where the nutrient flux density is increased by different fertilization regimes.

Laboratory experiments

The laboratory experiments were carried out to estimate mineral nutrient requirements under different nutritional conditions: at maximum growth rate (Ingestad, 1979b), at varied nitrogen stress (Ingestad, 1979a, 1980; Ingestad & Lund, 1979; Ericsson, 1981a), or at varied stress of all nutrients in fixed proportions (Ericsson, 1981b; Ingestad, 1981). It was shown that the mineral nutrient requirements may be expressed as the nutrient proportions to be used and the relative rate of addition of such a nutrient set which is required to maintain a corresponding relative growth rate. When such nutrient additions were performed, at different relative rates, the relative growth rate obtained was strongly and linearly correlated to the relative addi-

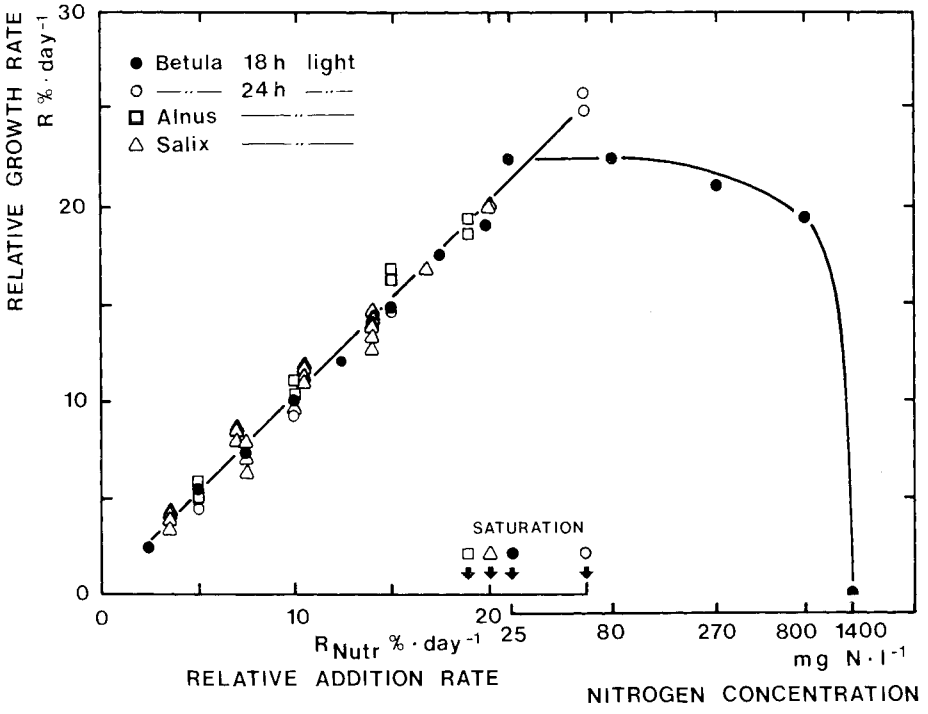


Figure 1. Relationships between relative growth rate (% d.w. increase per day) and the external nutrient factor during the exponential period of growth of some broad-leaf tree species. Within the range of suboptimum and optimum nutrition (up to saturation) the relative nutrient addition rate is the driving variable and within the supra-optimum range the external concentration is efficient. (From Ingestad & Lund, 1979; Ingestad, 1980, 1981; Ericsson, 1981ab).

tion rate, a line passing close to the origin and at an angle of about 45° to the axes within the sub-optimum range and including optimum (Figure 1). The relationship was the same, independent of plant species or day length, but the maximum relative growth rate and thus the maximum utilizable relative addition rate varied with such factors. Thus, the line was cut off at optimum nutrition when the plant system may be regarded as saturated with nutrients and at different relative addition rates for different species and day lengths (Figure 1). At higher addition rates the nutrients were not taken up in proportion to the additions but the external concentration increased. Supra-optimum conditions were produced which subsequently led to growth reduction and lethality as shown in Figure 1 for birch seedlings grown in 18 h of light. Thus, the relationship between external and internal nutrient factors is not continuous over the whole range of nutrition but the driving variable for sub-optimum and optimum nutrition (the relative addition rate) is different from that for supra-optimum nutrition (external concentration). These results are in a sharp contrast to accepted knowledge on plant nutrition (cf. Ingestad, 1979a, 1981).

The experimental use of the variable relative nutrient addition rate may be regarded as a simulation under controlled conditions of a natural process (cf. Ingestad, 1981). The different nutrient amounts made available are similar to those reached by a root system which grows exponentially through soils with different nutrient delivery capacities (mineralization rates), where the soil is virtually completely depleted of nutrients close to the root surface. This is the generally accepted picture of the situation in soils and the characteristic behaviour of the plants in the experiments was also very similar to that under natural conditions. Thus, for instance, at stable internal nitrogen concentration visual deficiency symptoms disappeared in the plants, independent of the level of the nutrient status, just as the case in natural vegetation but in sharp contrast to the behaviour in classical experiments.

Thus, there is much evidence for the decisive importance of the addition or availability rate (the flux density) of nutrients for plant nutrition. The mineralization rate and the relative root growth rate and root morphology are important factors determining nutrient status and growth of plants under field conditions. Concentration of nutrients in the soil is apparently an inadequate descriptor, disregarding its reflection on the nutrient flux density at the moment. A substantially increased concentration because of a higher nutrient flux than uptake rate would, instead, mean a negative correlation with uptake rate because of increased risks of leakage and therefore loss of available nutrients and future nutrient flux. Furthermore, high salt concentrations are probably harmful to many organisms in an ecosystem and may therefore decrease utilization and retention of supplied nutrients. It follows that fertilization should be carried out to increase nutrient flux density and not the nutrient concentrations in the soil. The applied fertilizer amounts must therefore be of the same order as the current mineralization rate to be efficiently absorbed and utilized by the ecosystem. Such fertilization requires many small supplies during the growing season adjusted to the current uptake capacity.

Field experiment

A field experiment in a young Scots pine stand, comprising an irrigation and fertilization treatment with almost daily small dosages during the growing season, was started in 1974 within the SWECON Project (Aronsson *et al.*, 1977; Aronsson & Elowson, 1980). The nutrients were added to accumulate according to S-shaped curves, both during each season and over the whole experimental period, thus following a rough estimate of the mineralization patterns. The yearly dosages are shown in Table 1, together with some other treatment data for the irrigated and fertilized plots (IF-plots) and the control plots (0-plots).

The IF treatment produced a dramatic change in tree and vegetation development. It was noticed that the treatment did not harm sensitive vegetation but that even mosses and lichens were stimulated. This indicates that concentration of salts was never increased to

Table 1. Seasonal data on irrigation and fertilization of the IF-plots of the fertilization experiment (Aronsson *et al.*, 1977; Aronsson & Elowson, 1980). Other nutrients than nitrogen, macronutrients as well as micronutrients, were supplied in fixed proportions to nitrogen as shown to be required (Ingestad, 1979a). Fertilizations were carried out five days per week during the growing season.

Year	Period	Irrigation, mm	Precipitation, mm	Period	Nitrogen supply, $g \cdot m^{-2}$
1974	12/7–19/9	100	100	12/7– 9/8	7
1975	23/5–12/9	300	180	23/5–22/8	10
1976	20/5–18/9	300	250	20/5–20/8	15
1977	16/5–30/8	250	240	16/5–19/8	15
1978	23/5–12/9	220	320	23/5–12/9	20
1979	28/5–11/9	230	290	29/5– 7/9	20

higher levels in the soil and therefore could not have harmful effects on the soil microflora and fauna. Later on the field flora was dominated by *Chamaenerion angustifolium*. However, the closing pine canopy has started to depress the field flora completely.

In 1979 a first sampling of vegetation and soil was carried out (Table 2). Even though the results may be regarded as a first and rather uncertain estimate of the nitrogen budget, they may be used as a rough indication of the fate of the applied nitrogen. The added nitrogen has increased the nitrogen amounts in all fractions sampled, but relatively little in the mineral soil fraction. However, the estimate from this fraction is especially uncertain because of the large amounts present. The figures in Table 2 indicate a loss of fertilizer nitrogen of about 16 g $N \cdot m^{-2}$ (24%), but a large proportion of this amount may be present in the mineral soil. In any case, the amount of fertilizer nitrogen recovered (76%) may be regarded as high.

The nitrogen flux on the 0-plots is mainly the result of the mineralization of organic material in the humus layer. On the IF-plots the nutrient flux density is increased, initially by the fertilizer as such but later on also by the feed-back of fertilization on the mineralization rate because of the increased amount of litter.

Other nutrients than nitrogen, macronutrients as well as micronutrients, were supplied in agreement with the nutrient proportions found to be optimum in birch (Ingestad, 1979a, 1981), thus implying a somewhat high-

Table 2. Estimated nitrogen budget in the 0-plots and IF-plots of the fertilization experiment (Aronsson *et al.*, 1977; Aronsson & Elowson, 1980). The analysis values are from samples taken in May 1979. The total nitrogen supply 1974–1978 was 67 g $N \cdot m^{-2}$ (Table 1).

Pool	Analyzed	Estimated	g $N \cdot m^{-2}$		Fertilizer nitrogen	
			0	IF	g $N \cdot m^{-2}$	% of supplied
Tree biomass,						
above ground	x		3.0	12.2	9.2	14
roots		x	1.2	5.2	4.0	6.0
Ground vegetation,						
above ground	x		3.1	7.0	3.9	5.8
roots		x	1.3	3.0	1.7	2.5
Litter	x		4.8	10.8	6.0	9.0
Humus	x		33.6	52.8	19.2	29
Mineral soil, –40 cm	x		145.6	152.4	6.8	10
Total			192.6	243.4	50.8	76

er relative supply of potassium than required by conifers (Ingestad, 1979b). However, this is motivated by the fact that the complete ecosystem and not only the pines was intended to be fertilized to secure non-limiting nutrient availability to the ecosystem.

A model analysis

A simple model is used to elucidate the use of nutrient flux density as the driving variable for nutrition under field conditions. The model is restricted to the nitrogen effects but on the other hand the other nutrients can be expressed in fixed relations to nitrogen (Ingestad, 1979b, 1981), these relations being used in the IF treatment (Table 1).

The two most interesting dynamic processes, the turn-over of carbon and nitrogen, are entered in the model: the carbon dynamics of the trees and the nitrogen dynamics of the trees as well as of the soil (Figure 2). The following differential equations are used to define such a model:

$$\frac{dW}{dt} = (a - bW)N - fW \quad (1)$$

$$\frac{dN}{dt} = (U + qM)\,\frac{W}{W + w_m} - pfW \quad (2)$$

$$\frac{dM}{dt} = pfW + \frac{w_m}{W + w_m}\,(U + qM) - qM \quad (3)$$

where W is carbon in the needle biomass (g $C \cdot m^{-2}$), N is nitrogen in the needle biomass (g $N \cdot m^{-2}$), M is nitrogen in the needle litter (g $N \cdot m^{-2}$), U + qM is the nitrogen flux density (g $N \cdot m^{-2} \cdot y^{-1}$) consisting of a mineralization rate (qM) and a nitrogen fertilization rate (U). Lower case letters denote parameters (Table 3).

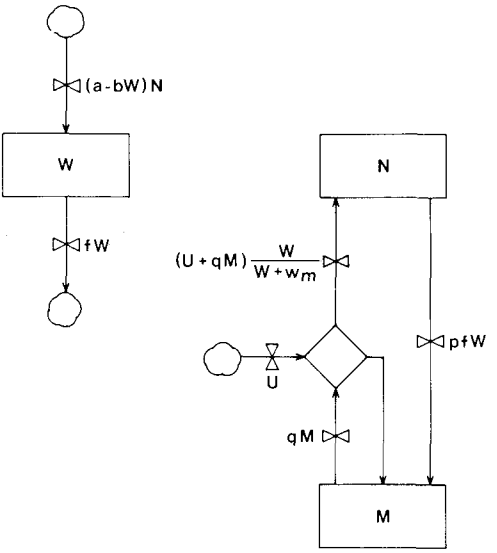


Figure 2. Flow-chart of a model based upon the *nutrient flux density concept*. The nutrient flux density, which determines the nitrogen uptake rate $\left(\frac{dN}{dt}\text{, see equation (2)}\right)$, is parted in a mineralization rate (qM) and a fertilization rate (U). W and w_m are the carbon amounts in the biomasses of pine needles and ground flora leaves, respectively. N and M are the nitrogen amounts in the pine needles and the litter, respectively. Lower case letters denote parameters. The dynamics of the model is formulated in equations (1), (2), and (3).

For simplicity, the parts of the ecosystem considered in the model are restricted to those having the most rapid dynamics, the needle biomass and the soil litter (fine root dynamics omitted, cf. Persson, 1978). Tree growth $\left(\frac{dW}{dt}\right)$ is described on the basis of the

Table 3. Model parameters.

Parameter	Estimated value	Dimension	Interpretation
a	20	g $C \cdot (g\ N)^{-1} \cdot y^{-1}$	Maximum nitrogen productivity
b	0.025	$m^2 \cdot (g\ N)^{-1} \cdot y^{-1}$	Reduction in nitrogen productivity due to increasing needle biomass
f	0.25	y^{-1}	Death rate of needles
h	0.04	g $N \cdot (g\ C)^{-1}$	Optimum nitrogen concentration in needles
p	0.008	g $N \cdot (g\ C)^{-1}$	Nitrogen concentration in dead needles
q	0.2	y^{-1}	Mineralization rate of needles
w_m	85	g $C \cdot m^{-2}$	Leaf biomass of ground vegetation

nitrogen productivity concept (Ingestad, 1979a, 1980, 1981; Ericsson, 1981ab). As a simplification the nitrogen productivity (a–bW) is assumed to be independent of nitrogen status, thus implying some overestimation of growth at low flux densities. The term (bW) implies a decreasing nitrogen productivity with increasing tree size (shading, water stress etc.). The losses of carbon (fW) and nitrogen (pfW) from the trees are given the simplest possible form, just being proportional to the amounts present.

The nitrogen uptake of trees $\left(\frac{dN}{dt}\right)$ is simplified as being in proportion to the fraction of needle biomass (W) of the total leaf biomass ($W + w_m$) when the utilization of the nitrogen flux density is described. The distribution of the fertilizer nitrogen (U) and the fraction delivered by mineralization (qM) are treated equally which is justified by the fact that fertilization is carried out by small, almost daily additions during the season. The nitrogen dynamics in the litter $\left(\frac{dM}{dt}\right)$ balances the turn-over of the needle biomass.

When the model is applied to laboratory experiments exponential growth is produced (as long as the trees are small, $W << a/b$) and with a linear relationship between nitrogen status and relative growth rate (cf. Ingestad, 1979b, 1980, 1981; Ericsson, 1981ab). However, the exponential period of growth is limited in time. In a nutrient solution with unchanged nitrogen addition rate the decreasing growth and uptake rate would result in an increasing external nitrogen concentration and supra-optimum conditions (Figure 1). In a field situation root growth rate and nutrient uptake rate would decrease with a diminishing capacity of the trees to utilize the nitrogen flux density. Finally, the trees will reach a stationary state with no further net growth of the needle biomass or net uptake of nitrogen. As long as no fertilizer is applied ($U = 0$) the soil will also be in a stationary state. The stationary values (index: s) for the pine stand are:

$$W_s = \frac{q}{pf} M_s - w_m \tag{4}$$

$$N_s = \frac{fW_s}{a - bW_s} \tag{5}$$

$$N_s + M_s = T_s \tag{6}$$

where T_s is the total available nitrogen pool in needles and litter. The maximum tree size (W_h) at stationary state occurs when the system is saturated with nitrogen and at optimum nitrogen concentration in the needle biomass (h). A further nitrogen fertilization cannot then be utilized and should be stopped. The stationary values under opimum conditions (index: h) are:

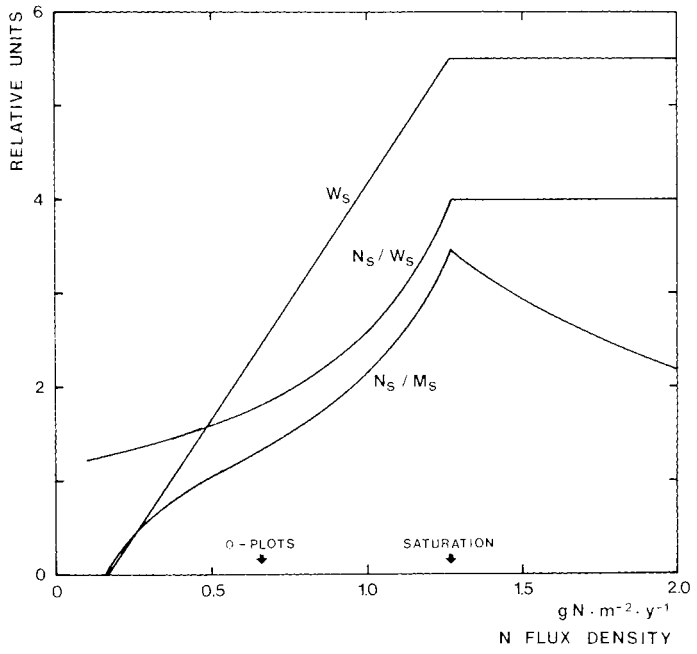
$$W_h = \frac{ah - f}{bh} \tag{7}$$

$$N_h = \frac{ah - f}{b} \tag{8}$$

$$M_h = \frac{pf}{bq}\left(a + bw_m - \frac{f}{h}\right) \tag{9}$$

This model can be applied to the field experiment discussed above if the parameters are estimated and such estimations may be based on data from the SWECON Project (Table 3). A typical life-time of Scots pine needles at the geographical location of the experiments is four years, giving $f = 0.25\ y^{-1}$. The minimum nitrogen concentration (ceasing growth; $\frac{dW}{dt} = 0$ in equation (1)) is about 0.6% of d.w., thus $a = 0.25/0.012 = 20$ g C · $(gN)^{-1} \cdot y^{-1}$ with a carbon content of 50% of d.w. (used also in the following estimates). The maximum leaf area index may be estimated to 5 and the weight/(leaf area) ratio to about 110 g C · m^{-2} giving $W_h = 550$ g C · m^{-2}. The optimum content of 2% N of d.w. needles gives $h = 0.04$ g N · $(g\ C)^{-1}$ and 0.4% N of d.w. in falling dead needles gives $p = 0.008$ g N · $(g\ C)^{-1}$. The value of b can be calculated from equation (7): $b = 0.025\ m^2 \cdot (gN)^{-1} \cdot y^{-1}$. The decomposition of needles was estimated to proceed at a rate of $0.2\ y^{-1}$ (Berg & Staaf, 1980) and the rate at which nutrients are mineralized may be estimated to be about the same, *i.e.*, $q = 0.2\ y^{-1}$. Persson (1975) gave an estimate of the leaf biomass of the ground vegetation to be about 170 g d.w. · m^{-2}, giving $w_m = 85$ g C · m^{-2}. In the beginning of the experiment (1974) the needle biomass was estimated to be about 60 g C · m^{-2} (Ågren

Figure 3. Stationary values of the needle biomass (W_s, 10^2 g $C \cdot m^{-2}$), the nitrogen concentration in the needles (N_s/W_s, 10^{-2} g $N \cdot (gC)^{-1}$), and the nitrogen ratio between needles and litter (N_s/M_s, at different values of the nitrogen flux density.



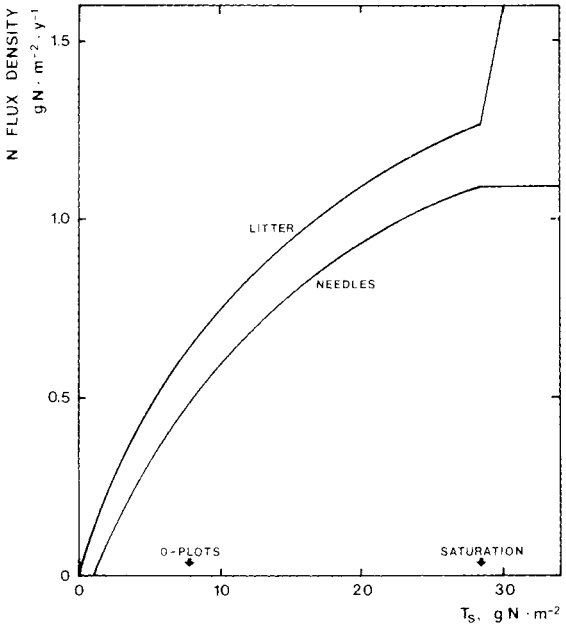


Figure 4. Stationary values of the nitrogen flux density through the litter (qM_s) and the needles (pfW_s) at different values of the total nitrogen pool ($T_s = M_s + N_s$).

et al., 1980) and consequently a nitrogen content of 1.2% of d.w. (Aronsson *et al.*, 1977) means a nitrogen amount in the pine needles at the start of $N_0 = 1.44$ g $N \cdot m^{-2}$. In 1979 the nitrogen amount in the needles and litter (N and M) was 3.0 and 4.8 g $N \cdot m^{-2}$, respectively (Table 2, 0-plots), giving $T = 7.8$ g $N \cdot m^{-2}$ and $M_0 = 7.8 - 1.44 = 6.36$ g $N \cdot m^{-2}$.

Finally, the fertilization on the IF-plots may be described by the function (only the fraction entering M and N is counted):

$$U_t = U_0 \cdot e^t \qquad (10)$$

with $U_0 = 1.6$ g $N \cdot m^{-2} \cdot y^{-1}$ and $\mu = 0.25$ y^{-1}. The fertilization is stopped when the saturation level is reached.

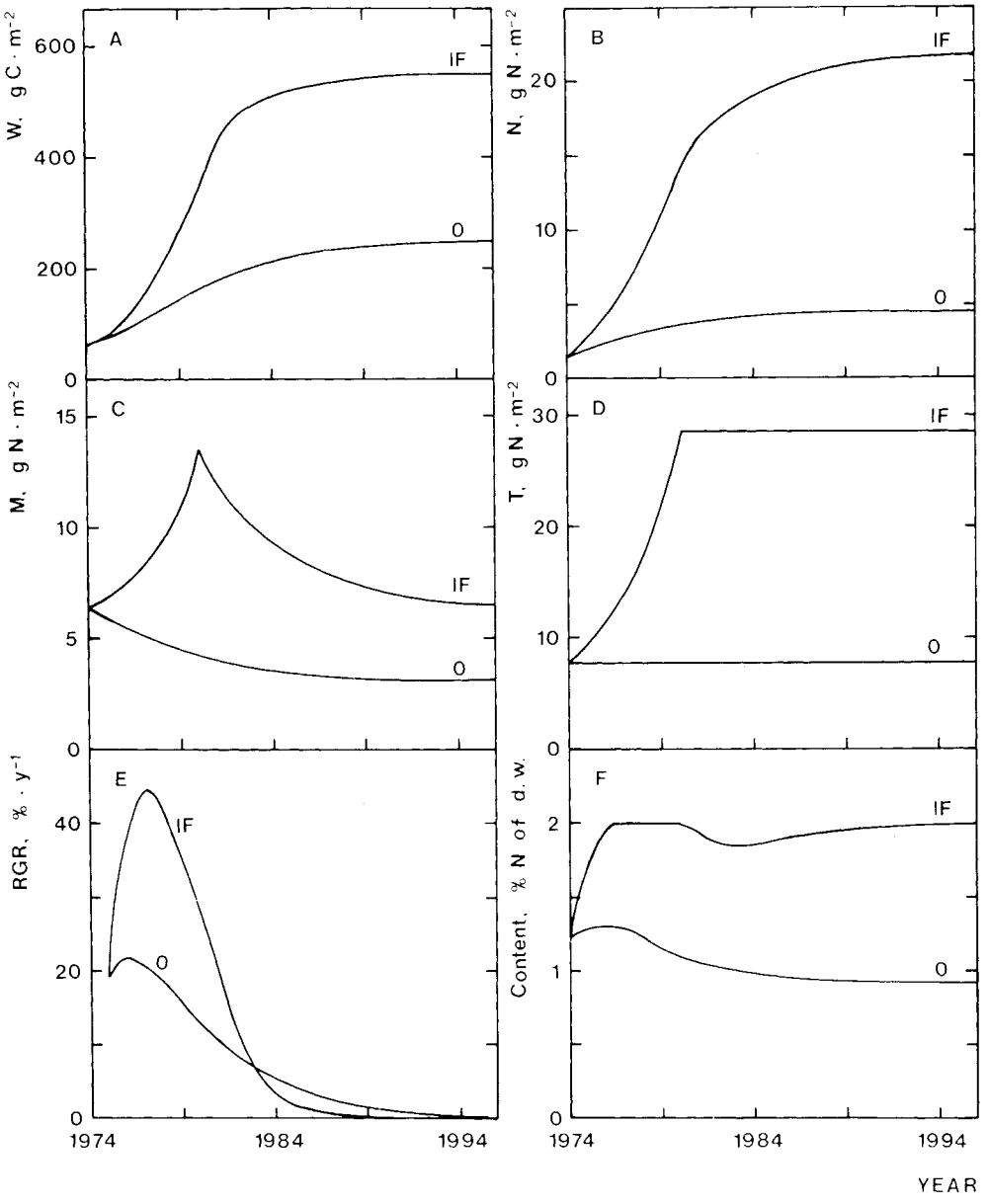


Figure 5. Simulation of the dynamics of the needle biomass (A), the nitrogen pool in the needles (B), the soil (C), and totally (D), the relative growth rate (E), and the nitrogen content in the needles (F), in control plots (0) and irrigated and fertilized plots (IF) of a field trial (Aronsson *et. al.*, 1977; Aronsson & Elowson, 1980).

The stationary values, with the estimated parameters, are related to the stationary nitrogen flux density (qM_s)) through equations (4) and (5) as shown in Figure 3 and the relationships between qM_s and the total nitrogen pool in needles and litter (T_s) is shown together with the nitrogen flux through the needle biomass (pfW_s) in Figure 4. It is seen that the 0-plots, where $T = 7.8$, would reach a nitrogen flux density of about 0.63 g $N \cdot m^{-2} \cdot y^{-1}$ (Figure 4). This corresponds to a needle biomass of 240 g $C \cdot m^{-2}$ (a leaf area

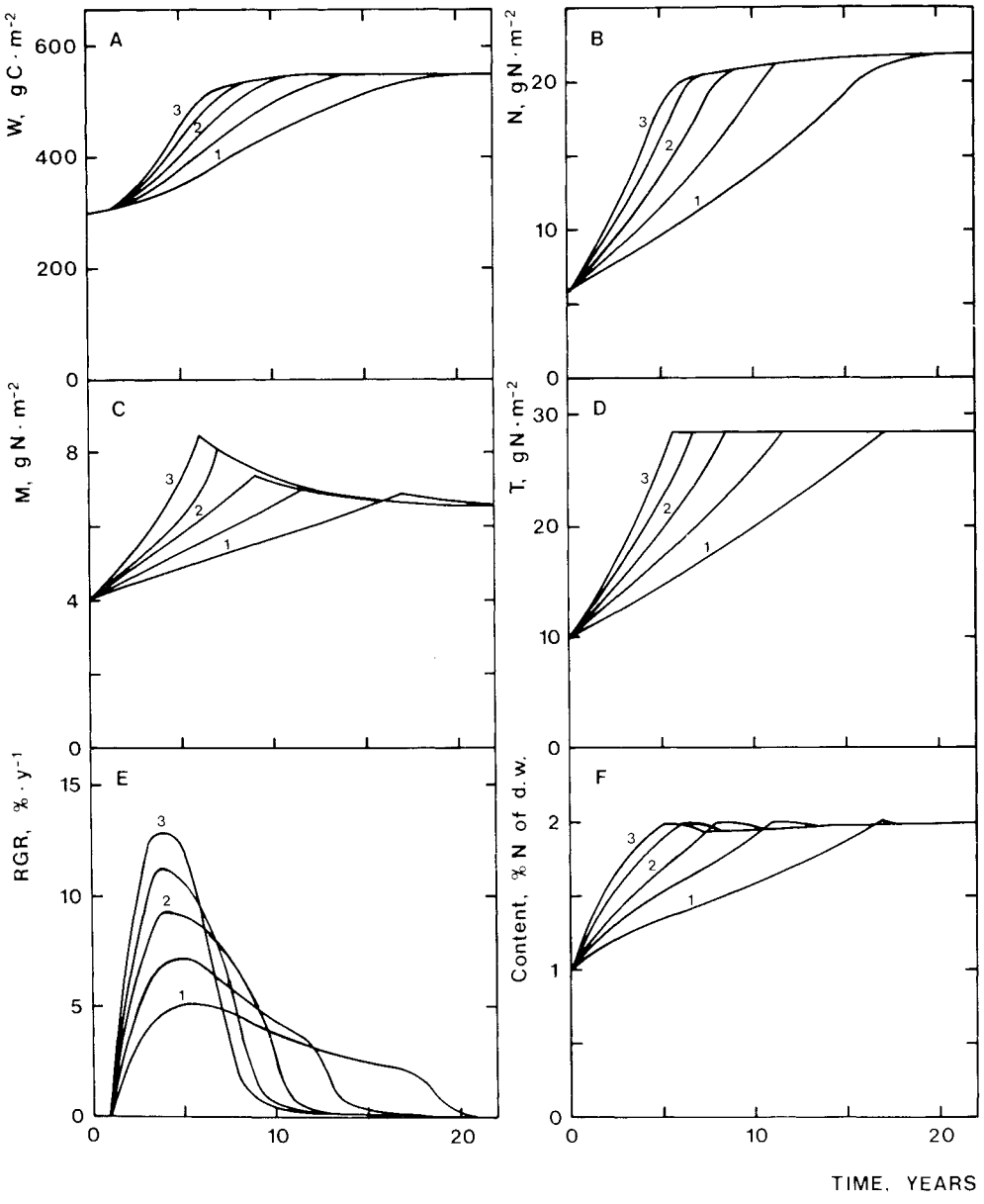


Figure 6. Simulation of the dynamics of biomass and nitrogen (A–F as in Figure 5) in a pine ecosystem in stationary state, starting with a total nitrogen pool of 10 g $N \cdot m^{-2}$, and with 1, 1.5, 2, 2.5, and 3 times as high fertilization rate (U) as the mineralization rate (qM).

index of 2.2) and a nitrogen concentration in the needles of 0.018 g $N \cdot (g\ C)^{-1}$ (0.9% of d.w.) as stationary values (Figure 3). These values are fully realistic.

In a saturated system the total amount of nitrogen in the pool (T_h) should be 28.4 g $N \cdot m^{-2}$ according to equations (8) and (9) (see Figure 5D). Since T = 7.8 in the 0-plots, 20.6 g $N \cdot m^{-2}$ has to be added before saturation is reached. The nitrogen content of the needles and litter on the IF-plots has increased (1978) by 15.2 g $N \cdot m^{-2}$ (about 23% of total supply,

Table 2) and thus an additional 5.4 g $N \cdot m^{-2}$ has to be supplied to this fraction. The nitrogen flux density would, according to the model, be about 1.3 g $N \cdot m^{-2} \cdot y^{-1}$ in the saturated system (Figures 3 and 4).

In Figure 5 the dynamics of the system is simulated by means of the differential equations (1), (2), (3), and (10) for the 0-plots and the IF-plots of the fertilization experiment. It is seen that the system should be expected to be saturated during 1980, which in fact seems to have occurred on the IF-plots. Later on there is only a redistribution of the total nitrogen pool (D) from the soil (C) to the needles (B), which in reality may require some further fertilization. This is also planned to be carried out. The maximum relative growth rate occurred in 1977 (E).

The model may also be used to simulate in a similar way the dynamic effects of various fertilization regimes. Thus, in Figure 6 the effects of different fertilization rates (U equal to 1, 1.5, 2, 2.5, and 3 times the mineralization rate, qM) have been simulated on a pine ecosystem starting in a stationary state with a total nitrogen pool of 10 g $N \cdot m^{-2}$. From equations (4), (5), and (6) the needle biomass (W_s) would be about 300 g $C \cdot m^{-2}$, nitrogen in the needles (N_s) about 6 g $N \cdot m^{-2}$, and nitrogen in the litter (M_s) about 4 g $N \cdot m^{-2}$. The leaf biomass of the ground vegetation (w_m) is set to 100 g $C \cdot m^{-2}$. It is seen that the process of saturation is strongly delayed if the fertilization rate is decreased. Figure 7 shows the number of years it takes to reach saturation with different fertilization regimes starting from different initial levels of fertility (nutrient flux density). However, the increased risks of leakage and decreased efficiency at high fertilization rates must be taken into consideration.

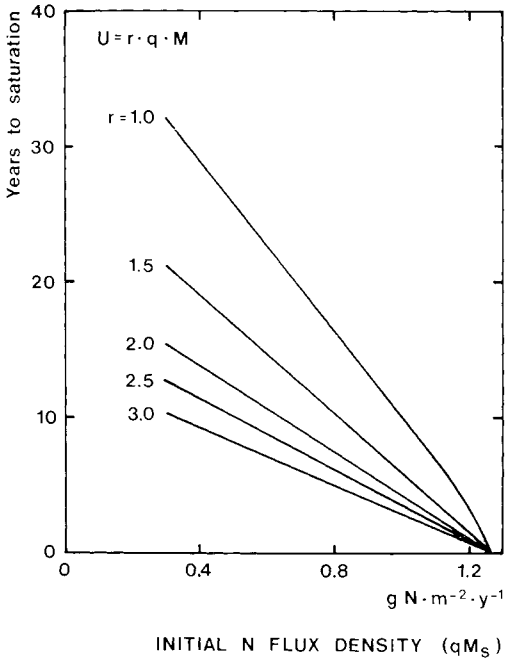


Figure 7. Time to reach saturation of a pine ecosystem in stationary state at different values of the initial nitrogen flux density (qM_s) and with 1, 1.5, 2, 2.5, and 3 times as high fertilization rate (U) as the mineralization rate (qM).

Conclusions

Reasonable results are obtained when the suggested model is tested on estimated data from ongoing experiments, whether the future development of the experimental ecosystem or different fertilization regimes are simulated. However, it must be remembered that the model is very simplified and that the required parameters are roughly estimated. Even though this is not the proper place to discuss in detail the figures arrived at or the consequences of the model, the analysis nevertheless shows that the model provides a possible way of evaluating fertilization effects with the feed-back on fertility (the mineralization rate) and production of coniferous ecosystems. Four main problems emanate from the analysis of the model, problems which should be investigated as soon as possible in field experiments, partly to get better estimations of important parameters and partly to elucidate some functions which appear to be of particular interest:

a) It is apparently of great interest to investigate possible fertilization regimes (Figures 6 and 7) with regard to the efficiency attainable with a minimum of fertilizer loss. Present knowledge cannot predict the fate of added nitrogen (nutrients) according to the different alternatives in Figures 6 and 7.

b) The functions and production of an ecosystem which is saturated with regard to

mineral nutrients (maximum production under the prevailing climate) can only very roughly be estimated with the proposed model but are of paramount interest for understanding of a highly productive forestry. Especially three factors appear to be important, *viz.* the size, the distribution, and the turn-over rate of the nitrogen and carbon pools in a saturated system.

c) The different nitrogren pools in the soil, their sizes and dynamics, need to be thoroughly investigated, especially when predicting the nitrogen dynamics in soil and vegetation in stands of different age or after a cutting.

d) The nitrogen (mineral nutrient) productivity concept needs to be studied in the field as well as in the laboratory to enable the more accurate analysis of the relations between nutrition and growth during tree development and also to permit correct analysis of the interface between biotic and abiotic processes in ecosystems.

Acknowledgements

The laboratory experiments were supported by grants from the National Council for Forestry and Agricultural Research in Sweden. The field experiment was carried out within the Swedish Coniferous Forest Project (SWECON), supported by the Swedish Natural Science Research Council, the Swedish Environmental Protection Board, the National Council of Forestry and Agricultural Research, and the Wallenberg Foundation.

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Amount and Quality of Information on CO_2-Exchange Required for Estimating Annual Carbon Balance of Coniferous Trees

S. Linder and T. Lohammar

Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden

Abstract

Possibilities of estimating the annual carbon budget from measurements of CO_2 exchange applied to a simple model of tree structure are discussed. It is suggested that this approach is particularly useful where estimates of root production are required. The accuracy of such an approach depends upon the number of samples of carbon dioxide exchange which are taken and it is discussed how these may be restricted in time and space.

Almost continuous measurements of CO_2 exchange were made on shoots of Scots pine by the use of temperature controlled assimilation chambers. The errors introduced for reduced sampling rates could then be estimated. There was a linear relationship between the number of days measured per week and the deviation between measured and estimated annual photosynthesis. From April to November two days of measurements per week were required to keep the error below ten per cent, five days per week to keep errors below five per cent. Measurement frequency can be reduced by using simple curve-fitting models to fill in days where measurements are lacking.

The spatial distribution of samples within trees is discussed. It is shown that more samples must be taken in denser grown stands because of the effects of the light climate upon the photosynthetic efficiency within the crown.

The influence of stem and coarse-root respiration upon the annual carbon balance is discussed and examples are given of the errors introduced in the estimates of an annual carbon budget for a young Scots pine if the period of measurements was shortened from a year to the six warmest months of the year.

Introduction

Classical methods of primary production study lack accuracy and in themselves do not provide an understanding of the mechanisms by which growth and production are achieved. However, whereas there have been a number of attempts to write simulation models for the carbon balance of plants and communities, their structural and quantitative accuracy have not been adequately checked (Ågren, 1981).

With modern techniques it is possible to measure photosynthesis and respiration under field conditions, something that is of great value when trying to understand the environmental effects upon primary production (cf. Larcher, 1969; Šestak *et al.*, 1971).

In the present report we discuss the possibility of using gas exchange techniques for determining the carbon flow within forest trees. The results and ideas presented are based upon field measurements of gas exchange of Scots pine (*Pinus sylvestris*) in Central Sweden (Linder & Troeng, 1980, 1981ab; Troeng & Linder, 1982ab).

When trying to estimate or model the carbon flow within a tree or an ecosystem some kind of structure indicating the main compartments and carbon flows is needed. A very simplified structure of a tree (Figure 1) will be used as a starting point. The structure contains four biomass compartments; (A) needles, (B) stem and branches, (C) coarse roots, and (D) fine roots. The flows of carbon

to and from these biomass compartments are shown in the model structure.

In this model we assume that the only carbon flow into the tree is via photosynthesis in the needles (1) and that reassimilation of carbon dioxide solved in the transpiration stream (Zelawski *et al.*, 1970) is an internal redistribution of carbon without any influence upon the carbon balance. There is no need to include gross photosynthesis even if this concept is included in a number of definitions of primary production (cf. Sestak *et al.*, 1970). Since the discovery of photorespiration the old definition of gross photosynthesis – net photosynthesis plus dark respiration – has lost validity. Photorespiration is an almost instant release of fixed carbon and is of no interest when estimating annual carbon budgets and primary production. Thus, gross primary production (PP_G) equals net photosynthesis (A_1) minus the respiratory losses (2) from each biomass compartment.

$$PP_G = A_1 - (A_2 + B_2 + C_2 + D_2) \quad (1)$$

The net primary production (PP_N) is the PP_G *minus litter fall* (4), *consumption* (5), *and exudation* of carbohydrates from the fine roots (D_6).

$$PP_N = PP_G - \\ - (A_4 + B_4 + C_4 + A_5 + D_5 + D_6) \quad (2)$$

The normal consumption of needles (Larsson & Tenow, 1980) and fine roots (Magnusson & Sohlenius, 1980) was reported to be low at the site investigated and can be excluded as having no effect upon the annual carbon balance although during years of outbreaks of insect attack the situation can be drastically altered. Similarly, whereas the amounts of exudates lost via the fine roots are of great importance to microorganisms in the soil, this process has to be ignored since no information is available concerning the annual amounts of exudates.

With these simplifications we have reduced our conceptual model for net primary production to contain four biomass compartments (A–D) and five processes: net photosynthesis (1), respiration (2), translocation (3), litter fall (4), and growth (7), and depending on the applied method it would now be possible to

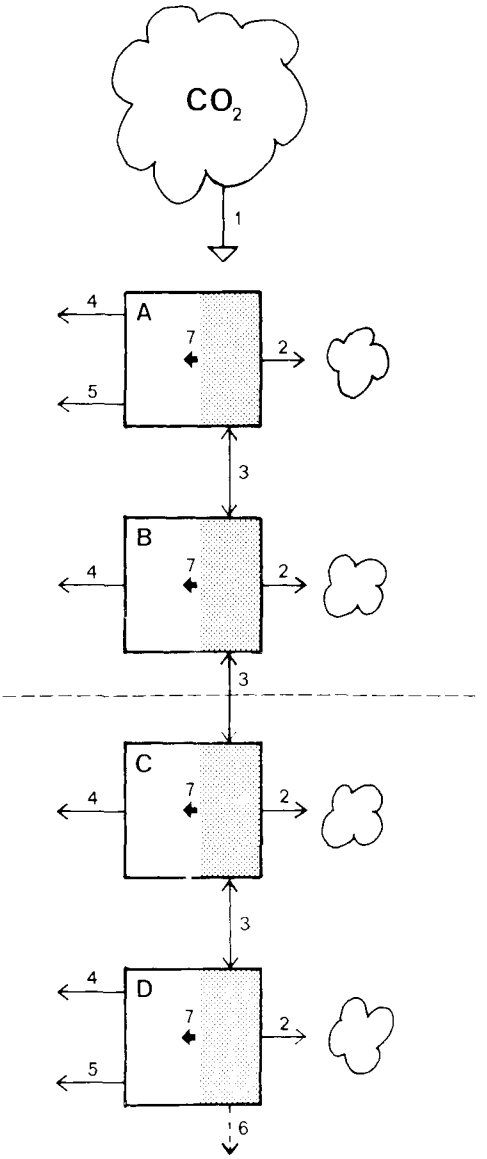

Figure 1. Schematic structure of a tree indicating the main compartments of biomass and flows of carbon. *Compartments:* (A) Needles and needle-bearing shoots, (B) Stem and branches, (C) Coarse roots, (D) Fine roots. The shaded area within each compartment indicates the labile carbonhydrate pool. *Carbon flows:* (1) Photosynthesis, (2) Respiration, (3) Translocation, (4) Litter fall, (5) Consumption, (6) Exudation, and (7) Growth.

estimate the PP_N using two or three of these processes.

Gas exchange techniques would require determination of net photosynthesis (1), respiration (2), and litter fall (4) (cf. Equations 1 and 2). When using harvesting methods the PP_N can be expressed as the sum of net change in each of the biomass compartments:

$$PP_N = (A_7 - A_4) + (B_7 - B_4) + \\ + (C_7 - C_4) + (D_7 - D_4) \quad (3)$$

Combining equations 2 and 3 gives an expression where PP_G can be described using one process, growth (7), only:

$$PP_G = A_7 + B_7 + C_7 + D_7 \quad (4)$$

From equations 1–4 it seems easier to determine PP_G and PP_N using the harvest methods (Equations 3 and 4) than by gas exchange techniques which have to be combined with litter fall measurements (Equations 1 and 2). However, because of the problems involved in estimating the production of below ground biomass (C and D) neither method offers an easy way to determine the annual carbon balance of the tree.

Theoretically both PP_G and PP_N could be estimated from measurements of translocation (3) and litter fall (4) (Figure 1). However, there are great problems in quantifying the carbon flow in translocation although qualitative information is of great help when trying to understand the dynamics of primary production (Ericsson, 1978, 1979).

The problems of measuring processes below ground make the definitions of PP_G and PP_N of theoretical rather than practical interest (Eq. 1–4). Coarse root production can be determined by harvesting methods and coarse root respiration can be estimated from measurements *in situ* (Linder & Troeng, 1981a) or on excised root sections (Kira, 1968). However, the high rates in turnover of fine roots (e.g. Ford & Deans, 1977; Persson, 1978) in combination with the almost impossible task of *in situ* measurements of fine root respiration in the field, are likely to introduce large errors in the estimates of the carbon balance. The problem of determining the amount of fine roots belonging to a certain tree will not facilitate the exercise (cf. Ågren *et al.*, 1980).

We therefore suggest that the amount of carbon used below ground is estimated from an analysis of the carbon balance of the aerial parts of the biomass. The amounts of carbon going below ground could then be derived from:

$$A_1 - (A_2 + A_7) - (B_2 + B_7) = \\ = (B \rightarrow C)_3 \quad (5)$$

Assuming that coarse root growth and respiration can be estimated, the allocation to the fine roots would be:

$$(C \rightarrow D)_3 = (B \rightarrow C)_3 - (C_2 + C_7) \quad (6)$$

The need of independent estimates of fine root production and fine root respiration for validation purposes is obvious when using equation 6.

Materials and methods

The results and calculations presented are based upon measurements of gas exchange in Scots pine (*Pinus sylvestris* L.) carried out in a 20-year-old stand at SWECONs main site at Jädraås, in Central Sweden.

Since 1974 the experimental stand has been irrigated and fertilized with the object of eliminating water and mineral nutrients as factors limiting growth. The experimental design was described by Aronsson *et al.*, (1977) and the structure of the stand before the treatments started by Flower-Ellis *et al.* (1976).

The trees used in the estimates of annual carbon balance were of mean height and diameter from one control and one irrigated and fertilized plot as determined by an inventory of trees in September 1978.

Gas exchange was measured continuously in up to 16 temperature controlled assimilation chambers (Linder *et al.*, 1980) throughout a five-year-period. A general description of the research programme on photosynthesis and respiration can be found in Linder & Troeng (1980).

Most of the information on photosynthesis (Troeng & Linder, 1982ab) and respiration (Linder & Troeng, 1981a) presented were collected during 1978. In most cases the assim-

ilation chambers were placed on current and one-year-old shoots on the third whorl. Stem and coarse root respiration rates were measured on the same trees as the photosynthesis.

Results and discussion

Seasonal variation in photosynthesis

In mild climates variation in photosynthetic efficiency during the year is small (Fry & Phillips, 1977) and the photosynthetic rate is related to environmental factors in a similar way throughout the year. However, in more extreme climates there is a pronounced seasonal variation in photosynthetic efficiency (cf. Larcher, 1969; Jarvis *et al.*, 1976; Tranquillini, 1979).

In Central Sweden the period of photosynthetic activity is approximately nine months per year (Linder & Troeng, 1980; Troeng & Linder, 1981a). Photosynthesis starts in March when the ground is still frozen and the only water available is from storage. The initial rates are very low and will not start to increase until the ground thaws in late April. However, even with access to water the rates remain low since the photosynthetic apparatus has been partly destroyed during winter and early spring (Martin *et al.*, 1980ab; Öquist & Martin, 1980; Öquist *et al.*, 1980). The recovery of full photosynthetic efficiency can take up to three months (Figure 2). After reaching full efficiency this level is kept rather constant until early autumn and will not drop until severe frosts occur (Bauer *et al.*, 1969; Troeng & Linder, 1982a). However, even in late autumn the main limiting factor for photosynthesis normally is low photon flux densities and not temperature (Linder & Troeng, 1980).

To estimate the annual photosynthetic production from field measurements involves an extensive measurement programme to cover the whole season. Therefore it is worthwhile to investigate the expected errors in annual estimates, based on measurements from a limited number of days. In the following we will not deal with the requirements on measurement frequency within the day for estimating daily photosynthesis but assume that daily photosynthesis was either measured or missing.

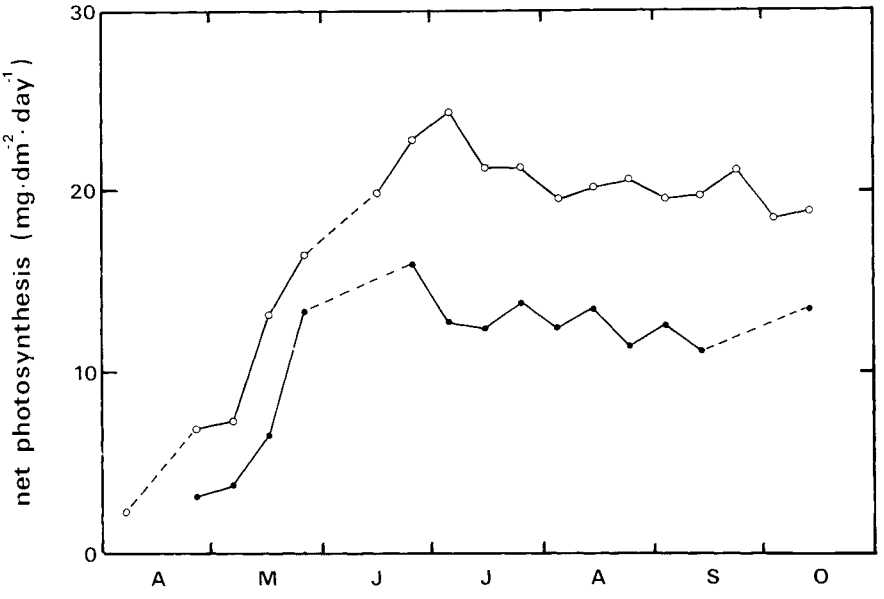

Figure 2. The seasonal variation in net photosynthetic rate of a one-year-old shoot of Scots pine at two different light levels within the temperature range 12–16°C. Filled symbols: 200–600 μE m^{-2} s^{-1}, open symbols >800 μE m^{-2} s^{-1}. Broken lines indicate that no values were found within the defined ranges.

The simplest prediction one can make from an incomplete set of measured days is to extend the values measured within a certain time period (e.g. week) to the whole period. The errors resulting from such an extension (compared with the "true" value from all measured days) are shown in Figure 3 for measurement frequencies, n, between one and six consecutive days per week. Since n consecutive days per week may be chosen in seven different ways it was possible to calculate a measure of the spread of the errors about the expected mean value (zero). This measure of spread was chosen as the mean of the absolute values of the errors (about 80% of the standard deviation for a normally distributed variable).

The relative error, expressed in per cent of the measured monthly value, had maximum values in spring and in the autumn. This is a result of the changes that occur in photosynthetic capacity during these periods. The absolute errors (mg CO_2 dm^{-2} day^{-1}), on the other hand, had minima in spring and late autumn as an effect of low photosynthetic rates. The relatively high errors obtained in June were probably an effect of the low number of measured days (23) in combination with a change in photosynthetic capacity with time (Figure 2). Applying the monthly estimated relative errors (Figure 3) to the monthly values (April – November) of photosynthesis of the "average" tree from a control plot (Table 1) gave an almost linear relationship between the number of days measured per week and the deviation from the measured photosynthetic production (Figure 4).

More than two days per week had to be measured from April to November to keep the error of the annual estimate below ten per cent and another three days of measurements were needed to come below five per cent. It should be noted that the errors presented are the average errors obtained when using the same number of days, or combination of days, as the number of days measured per month. Thus, the effect of single extreme days has been reduced in our estimates and

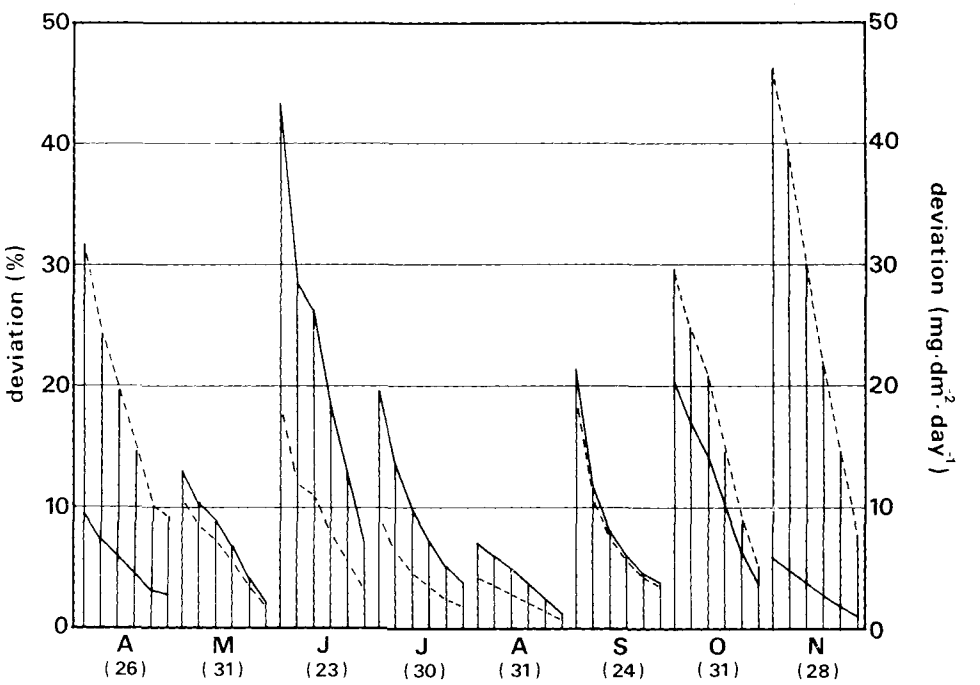

Figure 3. The absolute (solid line) and relative (broken line) errors when estimating monthly photosynthesis from April to November for a one-year-old shoot of Scots pine based on one to six measured days per week in the calculations. Figures within brackets give the number of days measured per month. For further details see the text.

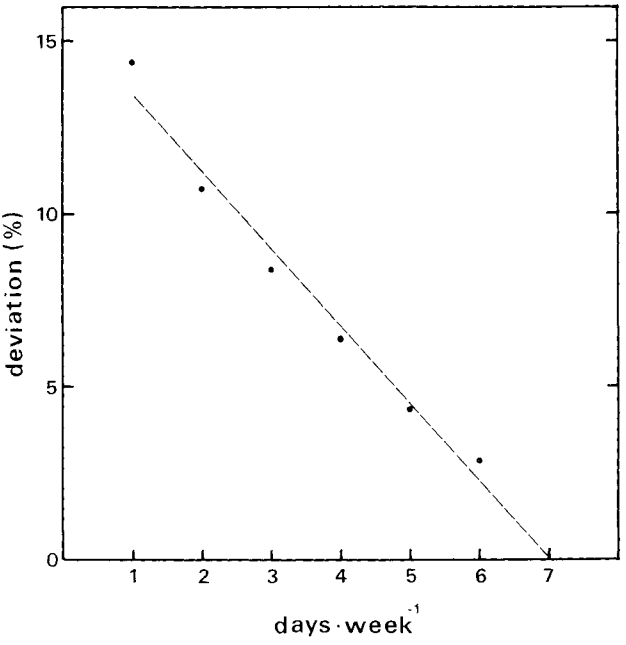

Figure 4. The relationship between the number of measured days per week and the error in the estimated value in per cent of the measured "annual" photosynthetic production (April – November). The values are based upon the monthly values of photosynthesis given in Table 1 and the error terms shown in Figure 3.

the calculated errors are probably underestimated compared to a real situation where a lower number of days is used to obtain an estimate of monthly photosynthesis.

97 per cent of the annual photosynthetic production occurred from May to October (cf. Table 1). Since the respiratory losses from the needle-bearing shoots during winter (December – February) and spring photosynthesis (March – April) were very low, the time span of intensive measurements could have been reduced to six months (May – October) without introducing large errors into the estimates of annual photosynthesis.

Table 1. The monthly photosynthetic production for different age classes of shoots in a 20-year-old Scots pine expressed as per cent of the annual photosynthetic production. The calculations are based upon the structure of an "average tree" from a control plot. Area of needles: current 122 dm^2; one-year-old 88.5 dm^2; two-year-old 52 dm^2 and three-year-old 11.5 dm^2. Total annual photosynthetic production was 1435 g C.

Months	Current %	one-year-old %	two-year-old %	three-year-old %	Total %
January	–	–0.2	–0.1	–0.0	–0.3
February	–	–0.1	–0.1	–0.0	–0.2
March	–	0.1	0.1	0.0	0.2
April	–	1.8	0.7	0.1	2.6
May	–	6.8	2.7	0.4	9.9
June	0.3	11.4	4.6	0.6	16.9
July	5.3	10.5	4.3	0.5	20.6
August	10.1	8.6	3,5	0.4	22.6
September	8.8	5.3	2.2	0.3	16,6
October	5.7	3.3	1.4	–	10.4
November	0.5	0.5	0.2	–	1.2
December	–0.2	–0.2	–0.1	–	–0.5
	30.5	47.8	19.4	2.3	100.0

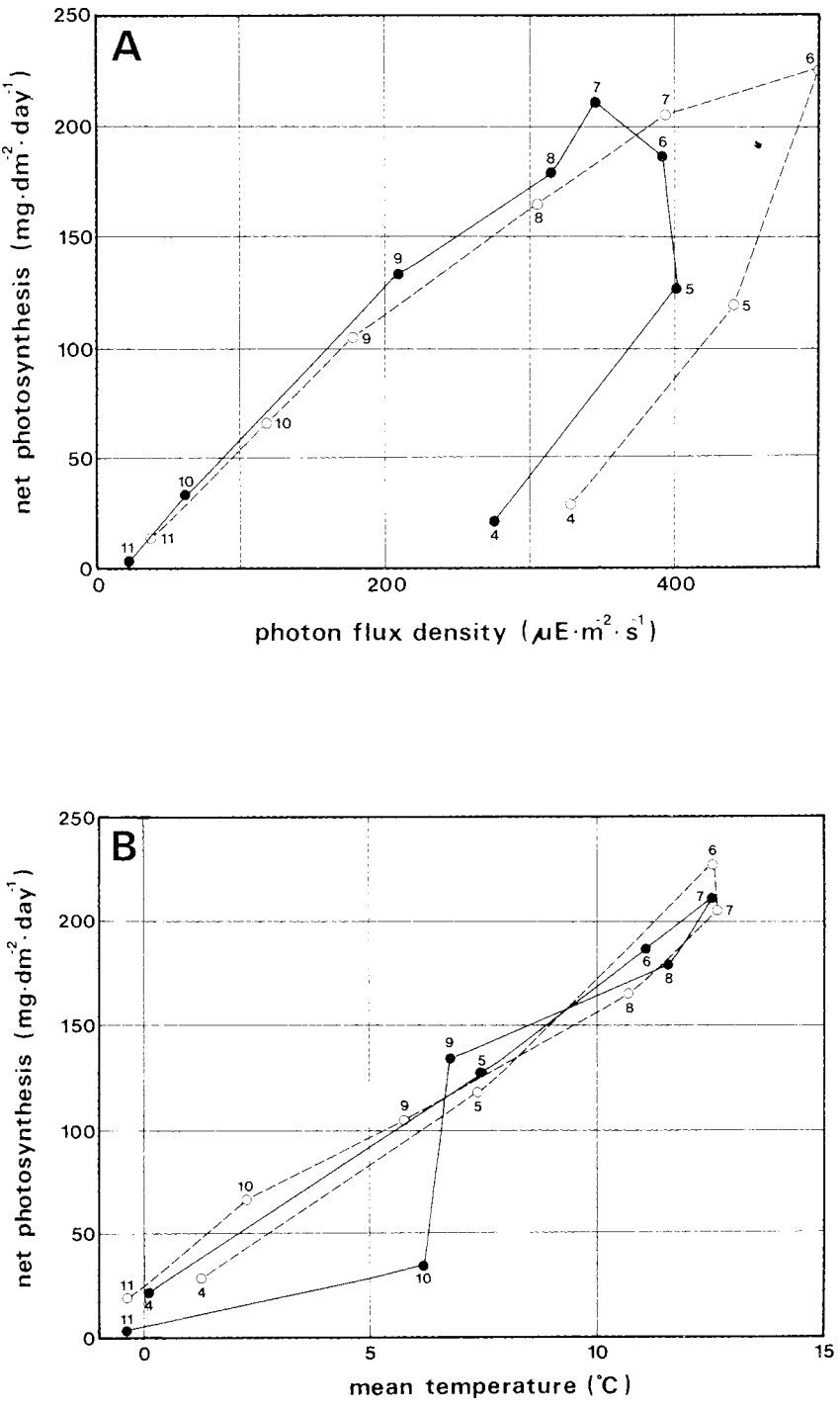

Figure 5. The average rate of net photosynthesis of a one-year-old shoot in Scots pine in relation to monthly mean photon flux density (A) and mean air temperature (B) from April to November, 1977 (solid line) and 1978 (broken line). The values presented are monthly means and the months are indicated in the figures by their respective numbers.

Before such a reduction in the time span of the measurements can be made, information about the seasonal variation in photosynthetic production is needed.

An alternative to the continuous measurements of net photosynthesis is to predict it by using an established model which simply requires meteorological measurements as inputs. There are a number of models available (e.g., Lohammar *et al.*, 1980; Hari & Kellomäki, 1981) which have good accuracy when photosynthetic efficiency is stable. As far as we know no simulation model exists which predicts changes in photosynthetic efficiency over the season from climatic variables. However, to be able to reduce 'direct measurement of net photosynthesis the next generation of simulation models of photosynthesis must take this seasonal variation into account. When plotting monthly values of mean photosynthetic rates against mean values in photon flux densities the problem of seasonal variation is clearly shown (Figure 5A). However, if the same rates of photosynthesis are plotted against monthly values of mean temperature an almost linear relationship is found (Figure 5B). Apart from October, 1977, which was warmer and more rainy than normal, two years seemed to follow the same general trend. This points to the possibility of predicting the seasonal change in photosynthetic capacity by using temperature records. However, this relationship has to be analysed in more detail before it can be of practical use.

The amount of measurements needed can be reduced if some kind of simple model is used to fill in gaps where data are missing. One week in September 1978 (Figure 6) was chosen to illustrate the effect of using two simple models to calculate weekly photosynthesis using records of photon flux density alone. Two types of light response curves were used, a Blackman type and a rectangular hyperbola function fitted to the data points (Figure 7). The initial slope of the Blackman curve was calculated by setting a light compensation point of 20 $\mu E\ m^{-2}s^{-1}$ and taking the average rate of photosynthesis between 20 and 400 $\mu E\ m^{-2}s^{-1}$ together with

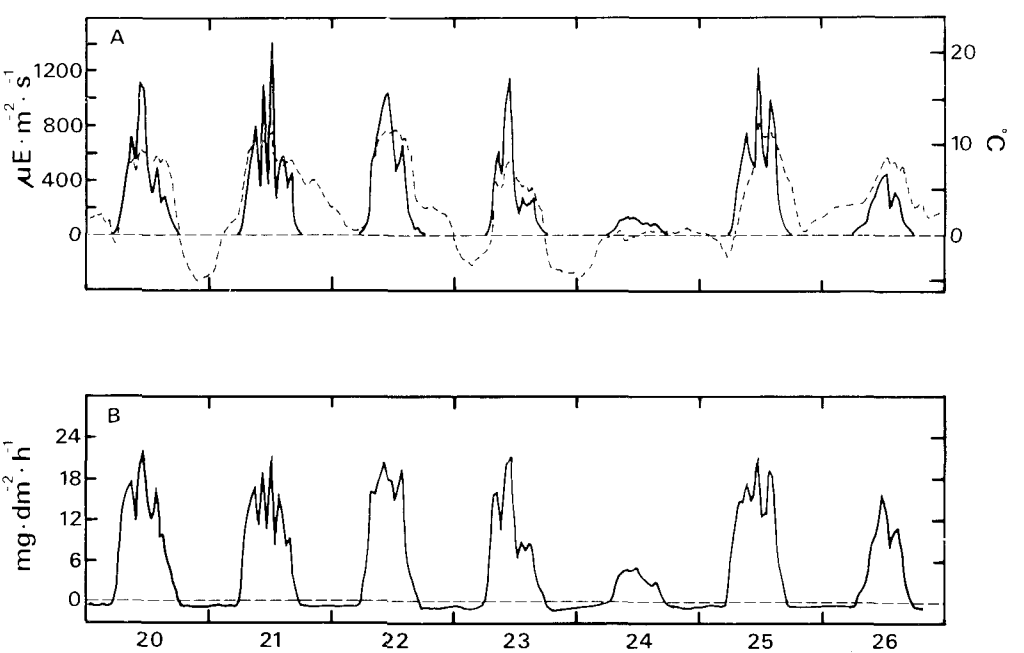

Figure 6. The diurnal course of (A): photon flux density (solid line), air temperature (broken line) and (B): net photosynthesis of a one-year-old shoot of Scots pine. The exemple is from a week in September 1978.

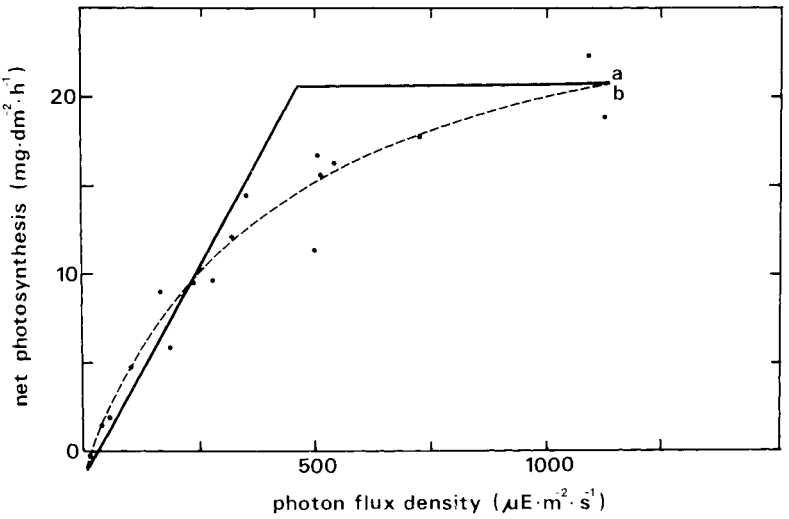

Figure 7. Light response curves of net photosynthesis estimated from values of net photosynthesis and photon flux densities measured on the September 20 (cf. Figure 5). (a): Blackman type of response curve, (b): Non-linear function fitted to the data points. For further details see the text.

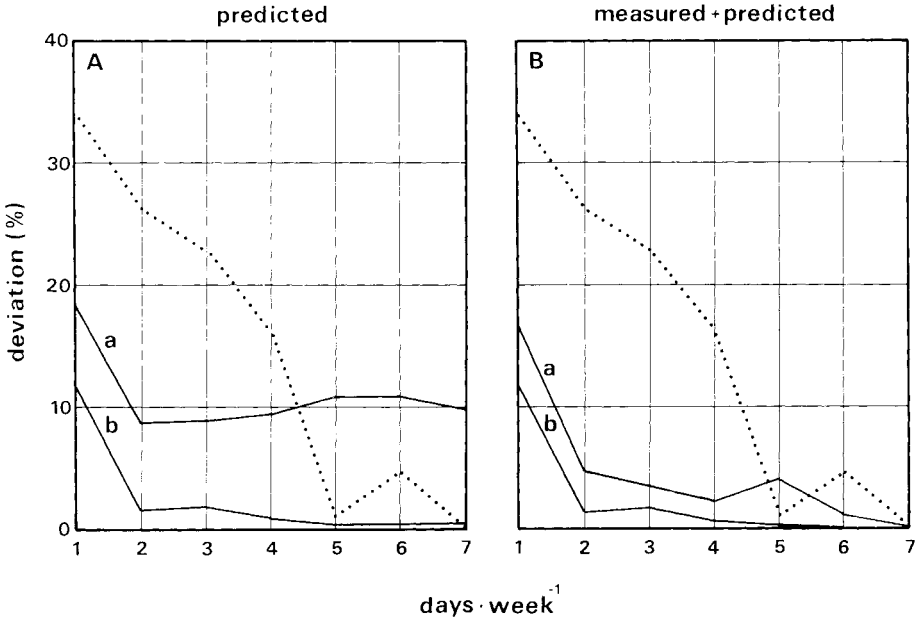

Figure 8. The deviation between predicted and measured photosynthesis during one week in September 1978 (Figure 5) using measured or predicted values or a combination of both. (A) The whole week is predicted by use of the functions in Figure 6 and the photon flux densities from Figure 5. The parameters were estimated using first one day's data and thereafter increasing with one day's data in each step. (a) Blackman curve, (b) Hyperbolic function. The dotted line shows a prediction based on actual measurements, starting with one day of measurements and then adding one day at a time. (B) Prediction of net photosynthesis where measurements are combined with predictions based on the functions in Figure 6 and photon flux densities from Figure 5. If two days were measured, the remaining five days were predicted to get the weekly value of photosynthesis. For further details see the text.

the mean photon flux density within the defined range. The rate at light saturation was taken as the average rate of photosynthesis above 800 $\mu E\ m^{-2}s^{-1}$. The parameters of the hyperbolic function were estimated using a non-linear parameter estimation programme.

In the first example the effect of increasing the amount of data used for parameter estimation was tested (Figure 8A). Prediction using the Blackman curve did not improve when more than two days of data measured were used to estimate the parameters. Prediction was within approximately ten per cent, which is the equivalent accuracy to directly measuring for more than five days per week. The hyperbolic function estimated from two days of data gave less then two per cent deviation from the true value, equivalent to direct measurement for six days in the week.

In the second example the effect of combining measured days with predictions to fill in gaps was tested (Figure 8B). Light response curves derived from the first day of measurements were used in the predictions (Figure 7). In this case the use of a simple Blackman curve brought errors down to less than five per cent. Already after two days of measurements the non-linear light response curve gave predictions that were within two per cent of the true value of weekly photosynthesis, as also found in the first example.

It is quite clear, thus that the number of measurements can be reduced to a large extent if a simple curve-fitting model is used to fill in gaps between direct measurements. However, records of photon flux density are needed for the entire period of interest to make the calculations possible and the measured days from which the parameters are calculated must cover the range of photon flux densities that occur during the actual period.

Variation within the crown

So far we have discussed the duration and frequency of measurements needed to minimize errors of annual estimates of photosynthetic production. The examples given have been from measurements of one-year-old shoots in one position of the crown (third whorl). To estimate the carbon balance of the whole tree then photosynthesis of the whole crown must be estimated.

The photosynthetic efficiency in needles of Scots pine after maturity decreases with age (Freeland, 1952; Künstle & Mitscherlich, 1975; Linder & Troeng, 1980). This, combined with a decreasing number of needles on older shoots, causes a pronounced reduction in photosynthetic production with increasing shoot-age (cf. Table 1). One-year-old needles accounted for 48 per cent of the total annual photosynthetic production for the "average" tree from the control plot although their needle area was only 32 per cent of the total leaf area. If no account had been taken of the differences in efficiency between age-classes and if the efficiency of one-year-old shoots had been used then net photosynthesis would have been overestimated by 11 per cent.

In the open stand where these results were obtained (leaf area index < 1) only small effects were found on photosynthetic capacity in relation to the position of shoots within the crown (Troeng & Linder 1982b). However, from closer stands of Sitka spruce (Jarvis *et al.*, 1976) and Norway spruce (Schulze *et al.*, 1977) pronounced effects of developmental position upon the photosynthetic efficiency have been reported. So before chamber measurements from one position in the crown are extended to the whole crown the variation in efficiency within the crown must be known.

Even without an effect of developmental position upon the rate of photosynthesis in different parts of the crown there are problems in estimating total crown photosynthesis because of the reduction in light within the canopy. There are many papers published on how to estimate light within canopies but there is no general and simple way to achieve a description of the light climate within a crown or a canopy of trees.

Using an empirical function for light reduction within the crown of the "average" trees from control and irrigated-fertilized plots we estimated the reduction in photosynthetic production caused by light reduction (Figure 9). This function was based upon light measurements above, within, and below the

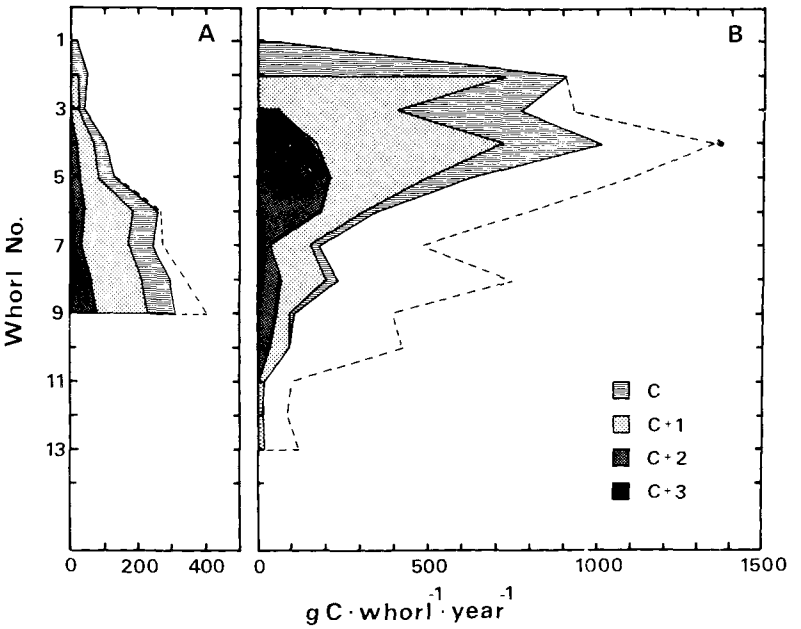

Figure 9. The distribution of annual photosynthetic production within the crown and between different age-classes of needles on "average" trees from a control plot (A) and an irrigated-fertilized plot (B) during 1978. The broken lines indicate the production figures obtained if no account is taken of the reduction in photon flux density within the canopy.

canopy from which an extinction coefficient was derived and thereafter used in Lambert-Beer's law to calculate the light climate for each whorl assuming that the whole canopy consisted of "average" trees. It was found that the error introduced in not taking the light reduction into account was 11 per cent on control plots and 41 per cent on irrigated-fertilized plots when using chamber measurements from the third whorl to estimate the annual photosynthetic production. For example photosynthesis of the lowest four whorls on the irrigated-fertilized tree was less than 20 per cent of what could be expected from the leaf areas if the light levels had been the same as on the third whorl (Figure 9B).

It is obvious from these simple examples that one of the major problems in estimating annual photosynthesis from chamber measurements is to describe the light climate within the canopy. Until there is a simple and general method to apply we suggest the use of an empirical light penetration model where the extinction coefficient is determined from measurements above and below the canopy and then combined with information on leaf area distribution within the canopy.

Respiration from shoots

The respiratory losses from needle-bearing shoots are included in the estimates of photosynthetic production and do not have to be estimated separately. During the winter months when no photosynthesis occurred, the respiration from the shoots was very low (Table 1) and had negligible influence upon the total carbon budget. In milder regions the respiratory losses from needles may be of such magnitude during winter time that the losses cannot be ignored.

Stem and coarse root respiration

Stem respiration (Johansson, 1933; Linder & Troeng, 1980, 1981a) and coarse root respiration (Linder & Troeng, 1981a) measured *in situ* under field conditions exhibit a pro-

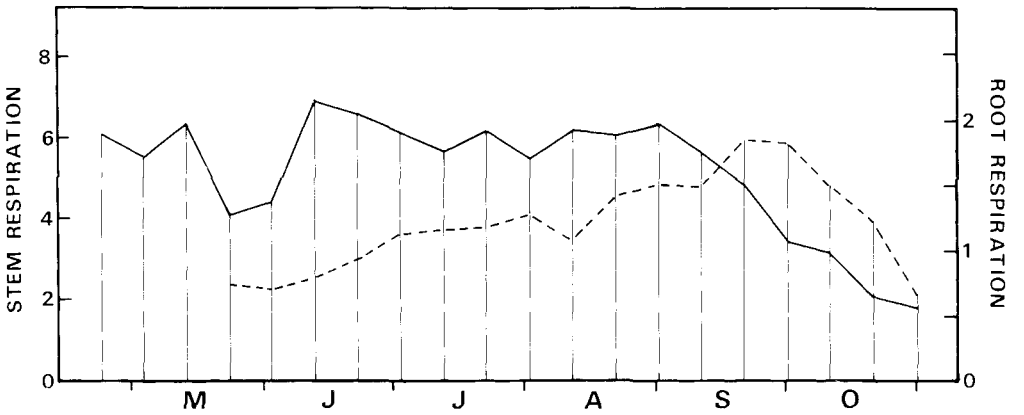

Figure 10. The seasonal course in respiration rates of stem (solid line) and coarse root sections (broken line) of a young Scots pine from April to October, 1978. The values are average rates per ten-day-period and are from the temperature range 7.5–12.5°C. At the end of the season the area of the enclosed stem was 4.4 dm^2 and that of the root 0.8 dm^2 (From Linder & Troeng, 1981a).

nounced seasonal variation. The performance of stem and coarse root respiration is mainly determined by the ambient air- and soil temperatures respectively, but is increased during periods of radial growth. The increased respiration rates are caused by higher respiratory activity (Figure 10), increase in respiring biomass per unit area and acclimation to prevailing temperatures (Rook, 1969; Strain *et al.*, 1976). For an annual carbon budget there is no need to separate the two components of respiration – maintenance and growth respiration – since the total respiratory losses are the ones of interest.

Stem and coarse root respiration can be measured *in situ* in the field by enclosing parts of the stem or the root in simple chambers (e.g., Linder *et al.*, 1980) or on cut stem and root sections under controlled conditions in the laboratory. If the cut stem surfaces are covered with paraffin wax there is a good agreement between results obtained in the laboratory and *in situ* measurements in the field. Since the Q_{10} of stem and coarse root respiration is very stable throughout the season (Linder & Troeng, 1981a) it would be possible to get good estimates of respiration from records of air and soil temperature in combination with respiration rates determined on cut sections in the laboratory at different times during the season (Figure 10). A linear relationship between mean temperature and respiration rate was reported for Norway spruce (Johansson, 1933) using weekly means of temperature and respiration rate. Similar results were obtained for Scots pine when using means for ten-day-periods (Linder & Troeng, 1981a). However, more data have to be analysed to test whether the relationship is the same from year to year.

The amounts of carbon lost in stem-, branch-, and coarse-root respiration were relatively low in the investigated stand; 3.3, 1.4, and 6.6 per cent respectively (Linder & Troeng, 1981a). However, the respiratory losses of carbon can be expected to increase with increasing tree age. Tranquillini and Schütz (1970) reported that 23 per cent of annual net photosynthesis was used in stem respiration in a 76-year-old *Pinus cembra* growing at the alpine timber line. They also estimated that up to 40 per cent could be lost via stem respiration in the warmer valleys. Compared with information on photosynthesis, little information is available on respiration under field conditions (Linder, 1979) and more knowledge is needed before we can evaluate the importance of respiratory losses in conifers.

The seasonal courses of stem and coarse root respiration were alike but the increase in root respiration occurred one month later in spring, and the decline in the autumn was

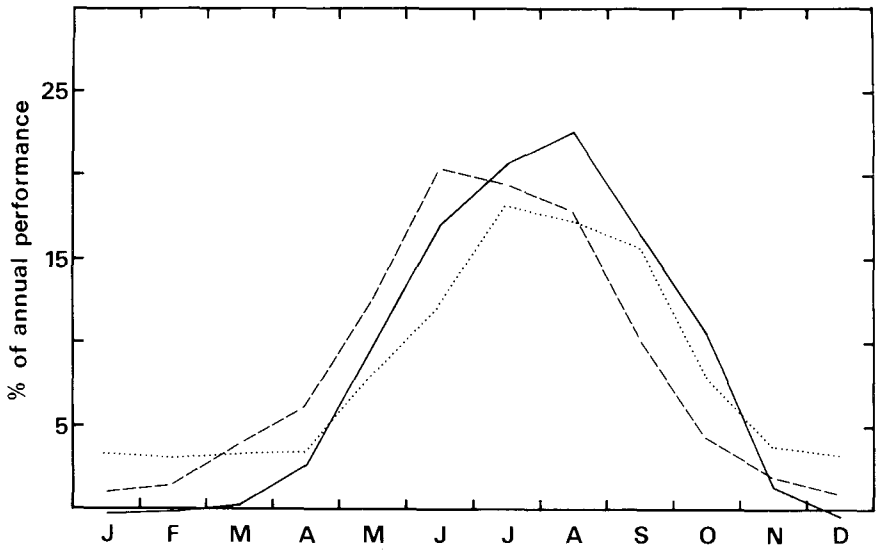

Figure 11. The seasonal course in photosynthesis (solid line), stem respiration (broken line), and coarse-root respiration (dotted line) of a 20-year-old Scots pine. The values presented are based upon a tree structure from a control plot. Root respiration during the winter was calculated using records of soil temperature. Absolute values: Photosynthesis (4976 g carbon), stem respiration (179 g carbon) and coarse-root respiration (326 g carbon) (From Linder & Troeng, 1981a).

also delayed by one month (Figure 11). If the measurements of stem and root respiration had been restricted to six months (May – October) the estimates would have underestimated the real values by 15 and 21 per cent respectively. Since the influence of respiration upon the annual carbon budget was small, the error in the annual budget would have been 0.5 and 1.4 per cent respectively if the six coldest months of the year had been ignored (cf. Figure 11).

Linder and Troeng (1981b) estimated the respiratory losses during cone development and showed that during years with large cone crops the cost of cone production – growth and respiration – may be of the same magnitude as the amount of carbon used for stem growth.

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